

A revision of the Antarctic genus *Chlanidota* (Gastropoda: Neogastropoda: Buccinulidae)

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Abstract.—The genus *Chlanidota* is revised to contain two subgenera, *Chlanidota* sensu stricto and *Chlanidota* (*Pfefferia*). *Chlanidota* s.s. has a broad distribution throughout the Antarctic region, and contains five species: *Chlanidota* (*Chlanidota*) *vestita* (Martens, 1881), *C. (C.) densesculpta* (Martens, 1885), *C. (C.) paucispiralis* Powell, 1951, *C. (C.) pilosa* Powell, 1951, and *C. (C.) signeyana* Powell, 1951. The subgenus *Pfefferia*, which differs from *Chlanidota* primarily in the morphology of its operculum, is endemic to South Georgia Island, and is known from three species: *Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908), *C. (P.) palliata* (Strebel, 1908), *C. (P.) invenusta*, new species. With its bulliform shell lacking a siphonal canal, the monotypic, circum-Antarctic genus *Neobuccinum* is conjectured to be the sister taxon of *Chlanidota*, but is readily distinguished by its smoother, higher-spired shell, radula in which the central cusp of the lateral teeth is medially placed, and a penis lacking a papilla.

The genus *Chlanidota* Martens, 1878, is one of the more diverse and wide-ranging members of the antiboreal buccinoidean radiation comprising the family Buccinulidae. As is true of nearly all buccinoidean higher taxa, this genus has been defined primarily on the basis of shell morphology, occasionally supplemented with observations of the radula and operculum. Consequently, neither the limits of this genus nor its relationships to other buccinoidean taxa have been well established.

Martens (1878) first proposed *Chlanidota* as a monotypic subgenus of *Cominella*, but later (Martens 1881) transferred the subgenus to *Buccinum* Linné, 1758. Watson (1886) included the type species of *Chlanidota* in the genus *Neobuccinum* Smith, 1877. Thiele (1912) erected the monotypic *Ficulina* as a subgenus of *Cominella*. Later, he discovered this taxon to be a junior syn-

onym of *Ficulina* Gray, 1867, and proposed *Notoficula* Thiele, 1917, as a new name. Still later, Thiele (1929:315) treated *Chlanidota* as a genus, and included *Notoficula*, *Pfefferia* Strebel, 1908, and *Bathydomus* Thiele, 1912, as subgenera. Powell (1951) elevated each of these subgenera to generic status, but regarded them to be closely related. Oliver (1983) showed *Notoficula* to be a neotenous eratoid rather than a buccinoidean.

Chlanidota has been treated most recently by Dell (1990), who included 13 species (Table 1), some tentatively, and noted that this genus has undergone an explosive radiation in Antarctic waters. He commented that the distributions, both geographic and bathymetric, “show puzzling patterns, especially through the Scotia Arc and adjacent regions of the Antarctic continent.” The closely related taxon *Pfefferia* (see Ta-

Table 1.—Listing of species attributed to *Chlanidota* and *Pfefferia* and their present taxonomic placement. Taxa listed in **bold** are valid species referable to these subgenera of *Chlanidota*.

<i>Chlanidota bisculpta</i> Dell, 1990	Not a <i>Chlanidota</i> . Belongs in an as yet undescribed genus.
<i>Chlanidota (Chlanidota) densesculpta</i> (Martens, 1885)	
<i>Chlanidota elongata</i> (Lamy, 1910)	Junior homonym of <i>Cominella elongata</i> Dunker, 1857; <i>Chlanidota lamyi</i> Dell, 1990 is a replacement name.
<i>Chlanidota eltanini</i> Dell, 1990	Not a <i>Chlanidota</i> . Belongs in an as yet undescribed genus.
<i>Chlanidota gaini</i> Lamy, 1910	Belongs in the conoidean genus <i>Belaturricula</i> .
<i>Chlanidota lamyi</i> Dell, 1990	Synonym of <i>Chlanidota signeyana</i> Powell, 1951
<i>Chlanidota</i> cf. <i>lamyi</i> Dell, 1990	Synonym of <i>Chlanidota signeyana</i> Powell, 1951
<i>Chlanidota (Chlanidota) paucispiralis</i> Powell, 1951	
<i>Chlanidota (Chlanidota) pilosa</i> Powell, 1951	
<i>Chlanidota polysperia</i> Dell, 1990	Not a <i>Chlanidota</i> . Belongs in an as yet undescribed genus.
<i>Chlanidota pyriformis</i> Dell, 1990	Synonym of <i>Chlanidota signeyana</i> Powell, 1951
<i>Chlanidota smithi</i> Powell, 1958	Synonym of <i>Neobuccinum eatoni</i> (Smith, 1875)
<i>Chlanidota (Chlanidota) signeyana</i> Powell, 1951	
<i>Chlanidota (Chlanidota) vestita</i> (Martens, 1881)	
<i>Chlanidota (Pfefferia) chordata</i> (Strebel, 1908)	
<i>Pfefferia cingulata</i> Strebel, 1908	Synonym of <i>Chlanidota (Pfefferia) palliata</i> (Strebel, 1908)
<i>Pfefferia elata</i> Strebel, 1908	Synonym of <i>Chlanidota (Pfefferia) palliata</i> (Strebel, 1908)
<i>Chlanidota (Pfefferia) palliata</i> (Strebel, 1908)	
<i>Chlanidota (Pfefferia) invenusta</i>, new species.	

ble 1), endemic to South Georgia Island, was last reviewed by Powell (1951), who selected a type species and added several new records for two of the four species described by Strebel (1908).

The present revision of the genus *Chlanidota*, which includes the subgenus *Pfefferia*, is based on a study of the large collections of these taxa sampled under the auspices of the United States Antarctic Program (USAP), as well as the type material of all species described or subsequently assigned to these taxa. The objectives of this study are: to assess the relationships among nominal taxa of *Chlanidota* and *Pfefferia* based on anatomical as well as conchological characters; to discern biogeographic patterns in the distribution of these taxa; and to begin to build a framework of anatomical data that can be used to resolve phylogenetic relationships of and among the buccinoidean taxa of the Southern Hemisphere.

Materials and Methods

This report is based primarily on the extensive collections of *Chlanidota* and *Pfefferia* (including dry shells and alcohol preserved anatomical material) collected by the United States Antarctic Program (USAP) and housed at the National Museum of Natural History, Smithsonian Institution (USNM). Additional material, including type specimens housed in the following institutions, were examined: BMNH—The Natural History Museum, London; MNHN—Muséum national d'Histoire naturelle, Paris; MNH-U—Museum für Naturkunde der Humboldt-Universität zu Berlin; SAM—The South Australian Museum, Adelaide; SMNH—Swedish Museum of Natural History, Stockholm; ZMH—Zoologisches Institut und Zoologisches Museum der Universität Hamburg.

In the material examined sections, "specimen" denotes alcohol preserved material,

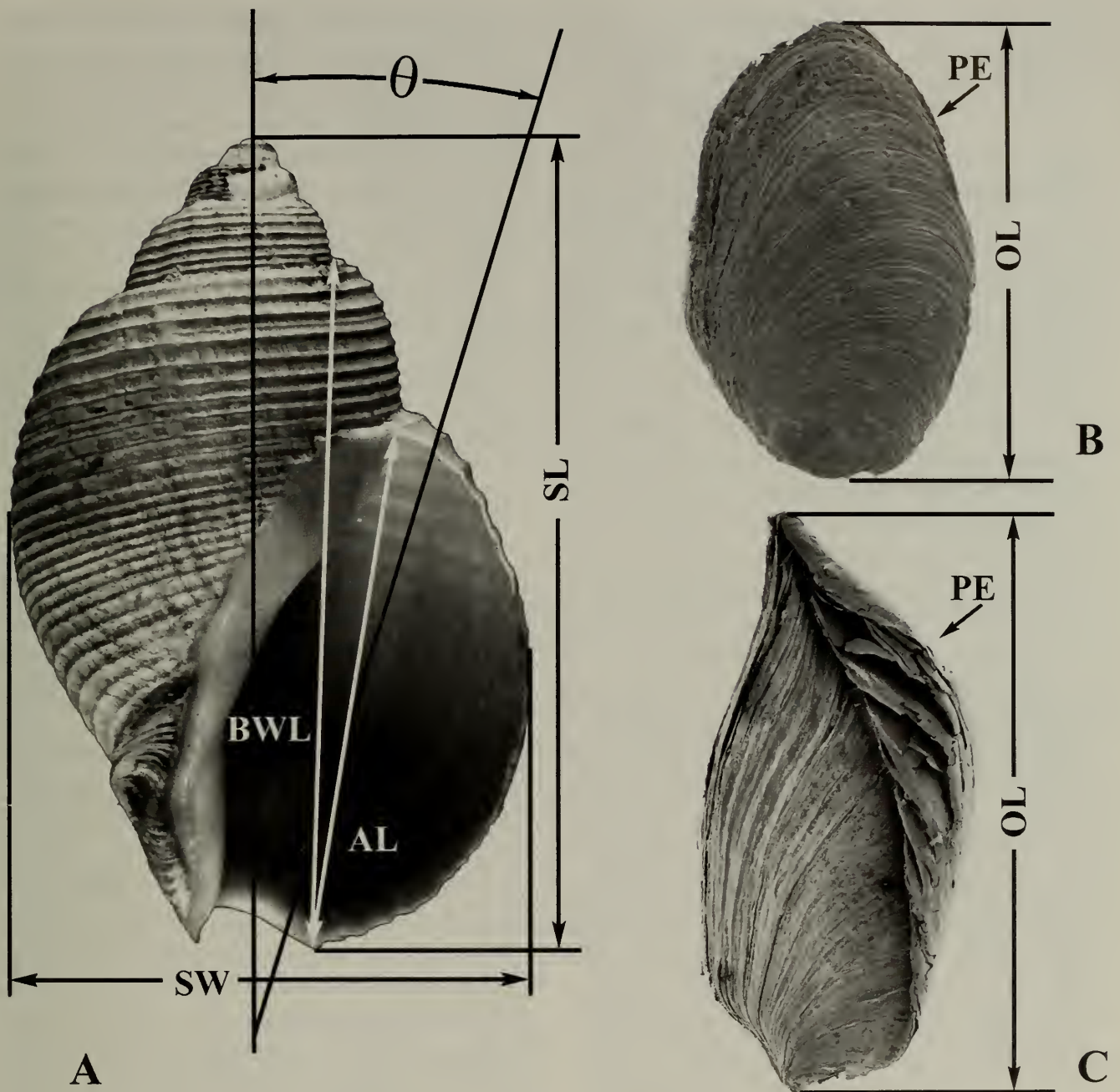


Fig. 1. Measurements of shell and operculum features. AL, aperture length; BWL, body whorl length; OL, operculum length; PE, posterior edge; SL, shell length; SW, shell width; θ , deflection of aperture from shell axis.

while “shell” refers to records containing only the empty shell.

Shell and operculum measurements were obtained for representative specimens of each species ($n = 10$, when available), as detailed in Figure 1. Shell ultrastructure was observed along freshly fractured surfaces parallel to the growing edge of the shell. Anatomical descriptions are based on gross dissections of preserved material. As the apex of the shell was strongly eroded in all specimens of *Chlanidota*, the aperture

length (AL) rather than the shell length was used as the reference when reporting the relative size of anatomical features. Radulae were removed by dissection, cleaned using diluted bleach (NaClO), coated with carbon and gold, and examined using a Hitachi S570 Scanning Electron Microscope (SEM).

Images were digitized using a Leaf Lumina Digital Scanning Camera. Optical and SEM images were processed using Photoshop Version 4.01 (Adobe).

Systematics

Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea
Rafinesque, 1815

The buccinoidean whelks comprise one of the few uncontroversial, monophyletic groups within the order Neogastropoda. While buccinoideans are readily identified on the basis of shell, radular, and alimentary system morphology (e.g., weakly sculptured shells lacking spines or columellar folds, lateral teeth with ≥ 2 cusps, absence of accessory salivary glands and rectal gland), there is no consensus as to the rank or inter-relationships of the group as a whole, or its constituent higher taxa (e.g., Thiele 1929; Wenz 1938; Bouchet & Warén 1985; 1986; Ponder & Warén 1988; Ponder & Lindberg 1996; Kantor 1996). As a result, most current classifications are of a typological rather than phylogenetic nature.

Based primarily on shell, radular, and opercular characters, Powell (1929) divided the Buccinoidea into the families Buccinidae, Neptuneidae, Buccinulidae, Cominellidae and Fascioliidae. In the same year, Thiele (1929) published an alternative and more widely accepted higher classification of the Buccinoidea, comprising the families Columbellidae, Buccinidae, Melongenidae, Nassariidae, and Fascioliidae. Powell (1951) subsequently revised his classification, regarding the Southern Hemisphere Buccinulidae (now including the subfamily Cominellinae) to be more closely related to the boreal family Neptuneidae than to Buccinidae. Ponder (1971) reviewed the New Zealand species of *Buccinulum* and concluded that anatomical differences did not justify their segregation from Buccinidae. Ponder (1974) and subsequently Ponder & Warén (1988) reduced the Buccinoidea to a family within Muricoidea, and also reduced in rank or synonymized most of the previously recognized families and subfamilies. Powell (1976) partially incorporated these demotions in taxonomic rank into revisions of his earlier work (e.g., Powell 1961), but

(Powell 1979:192) clearly continued to regard the Southern Hemisphere Buccinulidae to be distantly related to the Northern Hemisphere Buccinidae. Other authors have revised the higher systematics of the buccinoidean fauna of the Northern Hemisphere (Habe & Sato 1973) without treating austral representatives.

Pending a phylogenetic revision of the higher taxa within Buccinoidea, we provisionally retain the taxon Buccinulidae and its subdivisions, as understood by Powell (1951), to encompass the austral radiation of buccinoidean taxa.

Family Buccinulidae Finlay, 1928

Finlay (1928:250) proposed the family Buccinulidae (with subfamilies Buccinulinae and Siphonaliinae) and enumerated the included genera, but provided no diagnosis or differentiating characters. Powell (1929:57) suggested that Finlay's work was based on protoconch and teleoconch characters, and provided a modified classification "based primarily on the dentition." Powell (1951:151) further refined his concept of Buccinulidae, noting that the chief characteristics of the group were tricuspid rachidian teeth and an operculum with a terminal or subterminal nucleus. He subdivided the family into three subfamilies, the Cominellinae, Buccinulinae and Prosiphiinae based on the number of cusps on the lateral teeth.

Subfamily Buccinulinae Finlay, 1928

As refined by Powell (1951:151) the Buccinulinae are characterized by radulae with tricuspid rachidian teeth and tricuspid lateral teeth. The subfamily ranges from Antarctica to New Zealand, Australia, and along the eastern Pacific coast as far north as California.

Genus *Chlanidota* Martens, 1878

Powell speculated that *Chlanidota*, *Pfifferia* and *Neobuccinum* may represent a transitional stage between the short-ca-

nalled Cominellinae and the long-canalled Buccinulinae, the latter including the Antarctic genera *Probuccinum*, *Cavineptunea*, and *Bathydromus*. He included *Chlanidota*, *Pfefferia*, and *Neobuccinum* within Buccinulinae primarily on the basis of their tricuspid lateral teeth, but noted that in these taxa the intermediate cusp was likely the result of a bifurcation of the inner cusp.

Subgenus *Chlanidota* Martens, 1878

Cominella (*Chlanidota*) Martens, 1878: [Type (by monotypy): *Cominella* (*Chlanidota*) *vestita* Martens, 1878].

Chlanidota Thiele, 1929:314–315; Powell, 1951:139; Dell, 1990:177.

Description.—Shell medium-sized for family, reaching 25.5 to 42.6 mm, depending on species. Shell usually thin, fragile, ovate to elongate in outline, spire short to very short. Shell covered with thin to thick, smooth or hirsute periostracum. Spiral sculpture of either thin to very thin threads or of prominent cords. Aperture high, oval. Operculum very small (0.18–0.37 AL), ovate, coiled, with nucleus terminal, rotated to left, nearly perpendicular to long axis of operculum. Siphonal notch broad, dorsally recurved, siphonal fasciole with ridges along margins. Shell composed of 3 crystalline layers, outermost layer prismatic, middle layer of crossed-lamellar crystals with crystal faces comarginal (oriented parallel to growing edge), innermost layer of crossed lamellar crystals radial (oriented perpendicular to growing edge).

Digestive system generally typical of buccinids. Proboscis of medium length or long. Radular ribbon long, triserial. Rachidian tooth with arched base, straight sides, 3 large, robust cusps, usually of equal length. Lateral teeth with 3 cusps, outer cusp longest, middle cusp shortest, closely adjacent to innermost cusp. Salivary glands small, fused or separate. Valve of Leiblein large, well defined, lacking ciliary cone. Gland of Leiblein long, tubular, convoluted anteriorly, straightening and tapering pos-

teriorly. Oesophagus wide, muscular, with posterior crop-like enlargement lined with tall longitudinal folds. Stomach broadly U-shaped, without caecum.

Penis long, dorsoventrally flattened, with long, cylindrical terminal papilla, surrounded by deep circular fold at its base.

Remarks.—This subgenus is endemic to the Antarctic region. The highest diversity is in the Weddell Quadrant, especially in the vicinity of South Georgia Island. There are no records from the Ross Quadrant. Only *Chlanidota vestita*, the type species, extends northward beyond the Antarctic Convergence. The bathymetric range of *Chlanidota* sensu stricto is from 3 to 1116 m.

Chlanidota (*Chlanidota*) *vestita* (Martens, 1878)

Figs. 2–3; Table 2

Cominella (*Chlanidota*) *vestita* Martens, 1878:23; Martens, 1904:63; Thiele, 1904:168, Taf. IX, fig. 56 (radula); Lamy, 1911:pl. I, fig. 5.

Buccinum (*Chlanidota*) *vestitum* Martens, 1881:43–44, Taf. 9, Fig. 3a–c.

Chlanidota vestita Tryon, 1881:201, pl. 79, fig. 391; Smith, 1902:203; Powell, 1951:139; Carcelles, 1953:191, pl. 3, fig. 58; Powell, 1957:133; Powell, 1960:150; Dell, 1964:288; Gaillard, 1971:100; Cantero & Arnaud, 1984:68; Dell, 1990:184, fig. 311.

Neobuccinum vestitum Watson, 1886:216.

Description.—Shell (Fig. 2) small for genus (to 29 mm), thin, translucent, but strong, ovate in outline, with low, rounded spire. Protoconch unknown, upper teleoconch whorls heavily eroded. Teleoconch of up to 3½ evenly-rounded, convex whorls, deeply eroded where periostracum damaged or missing. Suture strongly impressed, forming extremely narrow channel between adapical spiral cord and previous whorl. Spiral sculpture of prominent but unequal cords, intervening spaces 2–4 times as broad as cords. Lectotype with 23 cords on body whorl, 8 on penultimate whorl. Para-

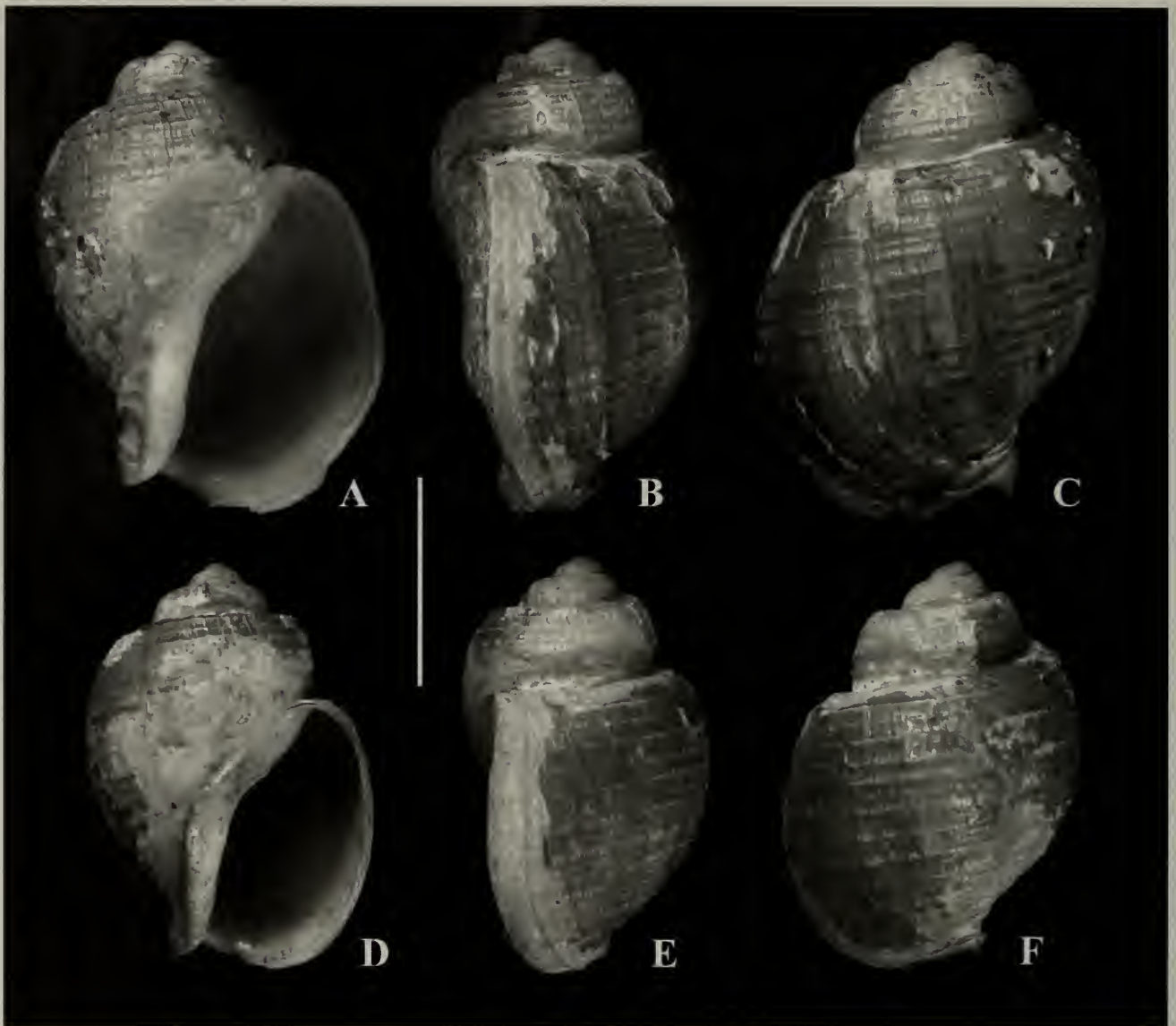


Fig. 2. *Chlanidota (Chlanidota) vestita* (Martens, 1878). A-C. Lectotype, MNH-U 25613-a (here designated). D-F. Paralectotype, MNH-U 25613-b. Both from Kerguelen Island. Scale bar = 1 cm.

lectotype with 22 cords on body whorl, 7 on penultimate whorl. Numerous fine, sinuated spiral threads between cords. Axial sculpture limited to growth lines, producing finely cancellate surface sculpture. Aperture broadly ovate, deflected from shell axis by 14–18°. Outer lip thin, evenly rounded, simple. Columella $\approx \frac{1}{2}$ AL, weakly concave, with strong siphonal fold. Parietal region, siphonal fasciole overlain by thin, grayish callus. Siphonal notch broad, dorsally recurved, with straight columellar, rounded apertural margins forming borders of fasciole. Ridge margin of fasciole runs from apertural margin of siphonal notch. Shell color chalky white, aperture weakly glazed. Periostracum thin, straw-colored,

smooth, glossy. Operculum, as illustrated by Dell (1990:fig. 311), very small (0.28 AL), ovate. Radula (Thiele 1904:fig. 56) with tricuspid rachidian and lateral teeth, as described for other species of *Chlanidota* illustrated herein.

Type locality.—Kerguelen Island.

Type material.—Two lots of syntypes, MNH-U 25613 (2 shells), MNH-U 25626 (3 shells). One specimen from MNH-U 25613, corresponding in size to the original description, is here designated as the lectotype (Fig. 2A–C). The remaining four specimens are paralectotypes.

Material examined.—The lectotype (MNH-U 25613-a) and one paralectotype (MNH-U 25613-b).

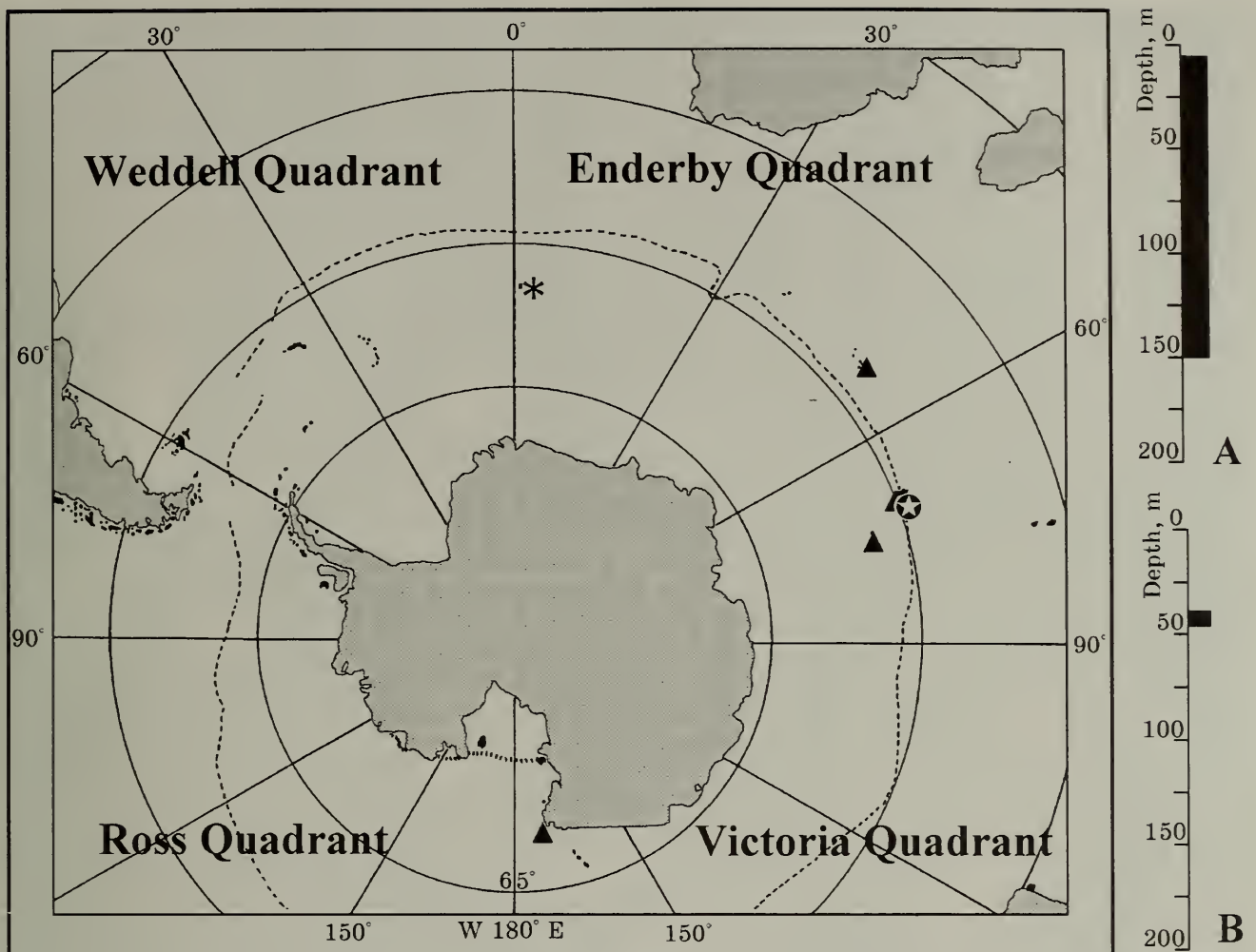


Fig. 3. Geographic distribution and bathymetric ranges of *Chlanidota (Chlanidota) vestita* (Martens, 1878), \odot = type locality, \blacktriangle = published records, and *Chlanidota (Chlanidota) pilosa* (Powell, 1951). * = type locality. A. Bathymetric range of *C. (C.) vestita* (Martens, 1878). B. Bathymetric range of *C. (C.) pilosa* (Powell, 1951). Antarctic quadrants follow terminology of Markham (1912). Dashed line indicates Antarctic Convergence.

Table 2.—*Chlanidota (Chlanidota) vestita* (Martens, 1878). Shell measurements of lectotype and paralectotype 1. Linear measurements in mm.

Character	Lectotype	Paralectotype 1
Shell Length (SL)	22.5	19.4
Body Whorl Length (BWL)	20.1	16.8
Aperture Length (AL)	17.1	13.3
Shell Width (SW)	17.1	14.5
BWL/SL	0.89	0.87
AL/SL	0.76	0.69
SW/SL	0.76	0.75
No. spiral cords on:		
Penultimate whorl	8	7
Body whorl	23	22

Published records.—*H.M.S. Challenger*: Sta. 149, Accessible Bay, Kerguelen, 49°08'S, 70°12'E, in 20–25 fm volcanic mud; Sta. 149B, off Royal Sound, Kerguelen, 49°28'S, 70°30'W, 25 fm, volcanic mud; Sta. 149D, off Royal Sound, Kerguelen, 49°28'S, 70°13'W, 28 fm, volcanic mud; Sta. 151, off Heard Island, 52°59'30"S, 73°33'30"W, 75 fm, volcanic mud (Watson, 1886). British, Australian and New Zealand Antarctic Research Expedition (BANZARE): Sta. 12, Off Grave Island, Island Harbor, Kerguelen, 5 m in red and brown algae; Sta. 58, Hydrography Channel, SE of Green Island, Kerguelen, in 50 m (Powell 1951). *R/V Southern Cross*: Cape Adare, Ross Sea, 43–47 m, BMNH (Smith 1902:203, see Dell 1990:fig. 311).

Table 3.—*Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1885). Measurements of shell characters. Linear measurements in mm ($n = 10$, holotype not included).

Character	Mean	σ	Range	Holotype
Shell Length (SL)	34.3	2.22	29.5–36.6	31.2
Body Whorl Length (BWL)	29.8	1.90	25.9–32.3	27.8
Aperture Length (AL)	24.4	2.18	20.6–27.8	24.4
Shell Width (SW)	23.2	2.20	18.7–27.2	24.5
Operculum Length (OL)	6.2	0.87	4.4–7.5	—
BWL/SL	0.87	0.01	0.85–0.88	0.89
AL/SL	0.71	0.03	0.67–0.75	0.78
SW/SL	0.68	0.04	0.63–0.74	0.79
OL/AL	0.25	0.04	0.18–0.31	—

Distribution.—Kerguelen, the Crouzets, Heard Island and the Ross Sea, in 5–150 m (Fig. 3).

Remarks.—*Chlanidota vestita* is readily distinguished from all congeners by its small, broadly shouldered shell, stepped spire, high body whorl, and moderately strong spiral cords.

In addition to the Kerguelen and Crozet Plateaus, records include a single report from Cape Adare on the Antarctic continent (Smith 1902). Dell (1990:184, fig. 311) examined and figured the Cape Adare specimen [BMNH], and confirmed it to be *C. vestita*, and not *C. smithi* as reported by Powell (1958). Dell (1964:288) reported *C. vestita* from Heard Island.

Chlanidota (*Chlanidota*) *densesculpta*

(Martens, 1885)

Figs. 4–7; Table 3

Cominella (*Chlanidota*) *densesculpta* Martens, 1885:91; Martens & Pfeffer, 1886:71, pl. 1, fig. 3a–f.

Chlanidota densesculpta Thiele, 1912:263; David, 1934:128; Powell, 1951:140, pl. 8, figs. 31–33; Carcelles, 1953:192, pl. 3, fig. 60; Powell, 1960:150; Dell, 1990 (partim):183, fig. 305, non fig. 306.

Description.—Shell (Fig. 4) large for genus (to 40.3 mm), thin, translucent, fragile, ovate in outline, with low, rounded spire. Protoconch unknown, early whorls heavily eroded. Teleoconch of up to 6 evenly-rounded convex whorls, deeply eroded

where periostracum damaged or missing. Suture impressed, obscured by thick periostracum. Spiral sculpture of numerous extremely fine spiral threads, broader than the spaces between them. Spiral threads sinuated, equal in strength, closely spaced (4–5 per mm), ~40 on penultimate whorl, >80 on body whorl. Axial sculpture limited to growth lines, producing finely cancellate surface sculpture appearing in places more like a rectangular array of fine pits. Aperture broadly ovate, deflected from shell axis by 9–13°. Outer lip thin, evenly rounded, slightly reflected. Columella <½ AL, weakly concave, with strong siphonal fold. Callus consisting of thin, silver-edged glaze overlying parietal region, siphonal fasciole. Siphonal notch broad, dorsally recurved, with straight columellar and rounded apertural margins that form borders of fasciole. Ridge margin of fasciole runs from apertural margin of siphonal notch, may be evident beneath columellar callus in some specimens. Shell color chalky white, aperture weakly glazed. Periostracum (Fig. 6C) thick, orange-tan, hirsute. Hair-like projections emanating from edges of lamellae at intersections of spiral threads with axial growth lines. Operculum (Fig. 4G–I, K) small (0.18–0.31 AL), broadly ovate, weakly coiled, with terminal nucleus (usually abraded) rotated nearly perpendicular to long axis. Attachment area nearly circular, spanning ¾ of inner surface, posterior, left margins thickened, glazed, abraded.



Fig. 4. *Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1875). A–C. holotype, MNH-U 37478. South Georgia Island. D–E, H, J. R/V *Islas Orcadas*, Sta. 20, Off South Georgia Island, 54°00'06"S, 37°40'36"W, in 68–80 m, USNM 906152. Periostracum of specimen in figure J removed with bleach to reveal spiral sculpture. F, G, I. R/V *Eltanin*, Sta. 1533, South Georgia Island, 54°00'S, 37°27'W, in 3–6 m. F. USNM 870722, G, I. USNM 896097. K. Operculum of specimen in fig. D. Scale bar = 1 cm for A–J, 2 mm for K.

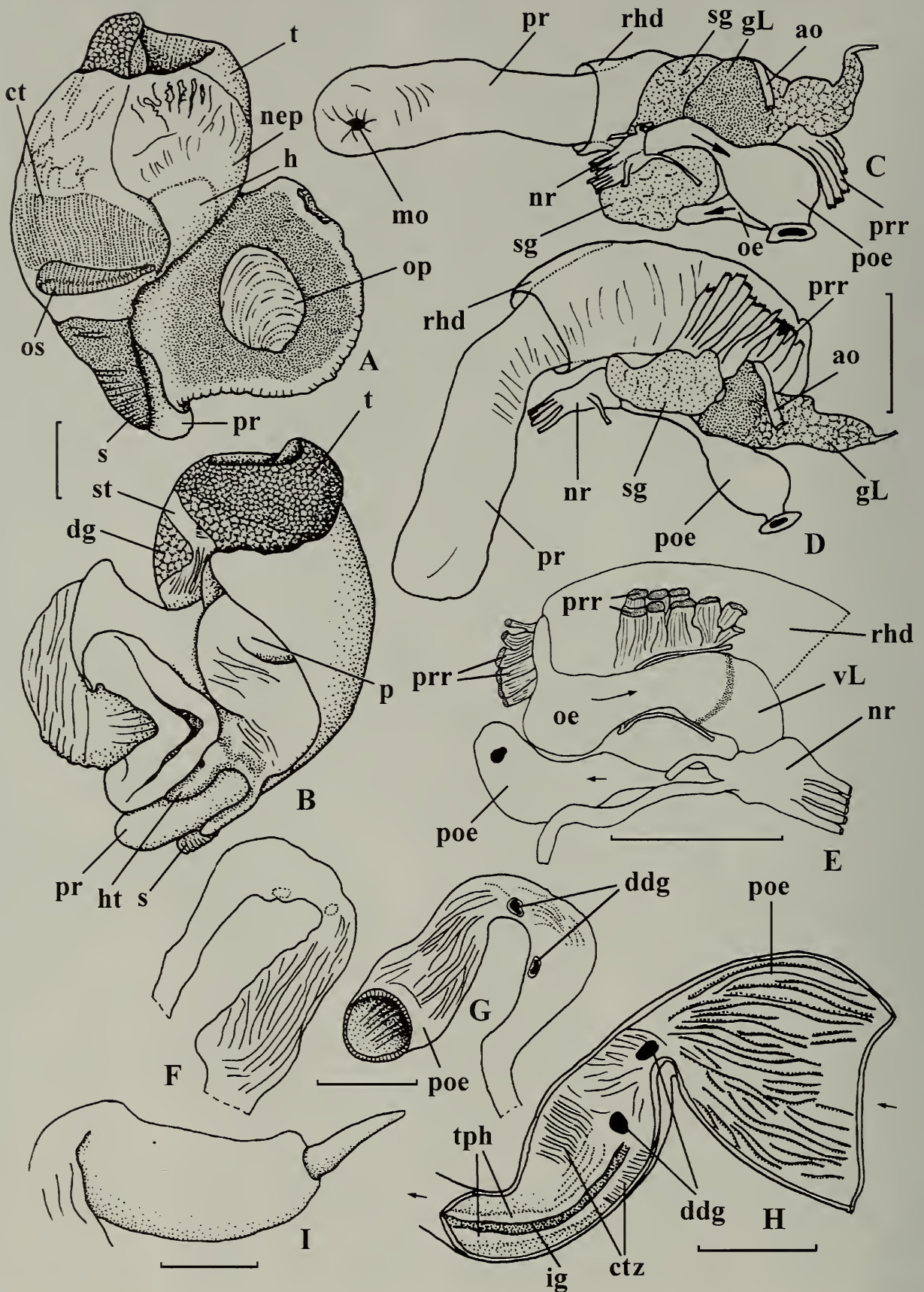


Fig. 5. *Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1875). R/V *Islas Orcadas*, Sta. 19, Off South Georgia Island, 54°01'42"S, 37°40'00"W, in 46–70 m, USNM 901651. A. Left, and B. right lateral views of ♂ animal removed from shell. C. Ventral and D. left lateral views of anterior alimentary system. E. Posterior portion of the proboscis, with salivary glands removed to show the valve of Leiblein. F. Dorsal, and G. ventral views of stomach. H. Stomach, opened mid-dorsally. I. Penis. Scale bars = 5 mm. Abbreviations: ao, anterior aorta; ct, ctenidium; ctz, compacting zone of the stomach; ddg, duct of the digestive gland; dg, digestive gland; gL, gland

Ultrastructure.—(Fig. 6D) Outermost layer prismatic ($\approx 90 \mu\text{m}$), middle layer comarginal crossed-lamellar ($\approx 140 \mu\text{m}$), inner layer radial crossed-lamellar ($\approx 32 \mu\text{m}$).

External anatomy.—(Fig. 5A–B). Soft tissues comprise approximately $2\frac{1}{2}$ whorls. Mantle cavity spans just under $\frac{1}{2}$ whorl, kidney $\frac{1}{4}$ whorl, digestive gland and gonad $1\frac{3}{4}$ whorls. Columellar muscle short, broad, attached to shell at rear of mantle cavity. Foot large, broadly rectangular ($L/W \approx 1-1.3$). Body base color yellowish tan, dorsal surfaces of the head, tentacles, siphon, foot mottled with dark grayish black. Head small, with broad, tapering tentacles, black eyes.

Mantle cavity.—Mantle edge smooth. Siphon of medium length ($\approx \frac{1}{3}$ AL), muscular, extending substantially beyond mantle edge. Osphradium greenish, bipectinate, with narrow axis, spanning about $\frac{1}{2}$ mantle cavity length. Ctenidium large, wide, spanning about $\frac{3}{4}$ mantle cavity length. Hypobranchial gland formed of few, distinct, widely spaced folds.

Alimentary system.—Proboscis smooth, unpigmented, of moderate length when retracted (≈ 0.6 AL), but long in semiprotracted position (≈ 1.1 AL; Fig. 5C, D). Proboscis sheath very thin-walled, translucent. Mouth opening forming triangular slit. Buccal mass muscular, large, filling retracted proboscis. Odontophoral cartilages paired, fused anteriorly, spanning $\frac{2}{3}$ of buccal mass. Radular ribbon long, 10.9–13.2 mm (0.47–0.52 AL), $\approx 540 \mu\text{m}$ wide (≈ 0.023 AL), triserial (Fig. 6A, B), consisting of 75–80 rows of teeth, posteriormost 5–7 teeth nascent. Rachidian teeth with 3 cusps on central portion of broad, anteriorly arched basal plate. Central cusp slightly

longer, narrower than lateral cusps. Lateral teeth with 3 cusps. Outer cusp stouter, nearly twice as long as inner cusp. Intermediate cusp slightly shorter than, immediately adjacent to inner cusp. Salivary glands small (Fig. 5C, D; sg), fused, dorsal to nerve ring, right salivary gland totally covering valve of Leiblein. Salivary ducts pass loosely along both sides of esophagus, becoming embedded in esophageal walls near rear of buccal mass. Valve of Leiblein well defined, large (Fig. 5E; vL), pyriform, without ciliary cone. Gland of Leiblein convoluted anteriorly, tapering posteriorly (Fig. 5C, D; gL), opening without constriction to mid-esophagus, just anterior to, left of crop (Fig. 5C; poe). Esophagus wide, muscular, enlarging posteriorly (Fig. 5C; poe) to form a crop-like structure lined with tall longitudinal folds. Stomach U-shaped, without caecum (Fig. 5F, H). Paired ducts of digestive gland closely spaced (Fig. 5H; ddg). Typhlosoles present (Fig. 5H; tph), poorly defined. Digestive gland clearly divided into 2 lobes. Zone of compaction well pronounced (Fig. 5H; ctz). Rectum terminates with well-defined anal papilla.

Female reproductive system.—Typically buccinoidean. Oviduct opens into medium-sized albumen gland. Ingesting gland single. Capsule gland large, occupies $\approx \frac{1}{2}$ of mantle cavity. Bursa copulatrix present, simple, hemispherical.

Male reproductive system.—Seminal vesicle of medium size, highly coiled. Prostate narrow, running along posterior half of mantle cavity wall. Penis dorsoventrally compressed, long ($0.8 \times$ mantle cavity length), with smooth walls, long, cylindrical papilla surrounded by deep circular fold around its base (Fig. 5I).

Type locality.—South Georgia Island.

←

of Leiblein; h, heart; ht, cephalic tentacles; ig, intestinal groove; mo, mouth; nep, nephridium; nr, circumoesophageal nerve ring; oe, oesophagus; op, operculum; os, osphradium; p, penis; poe, posterior oesophagus; pr, proboscis; prr, proboscis retractors; rhd, proboscis sheath; s, siphon; sg, salivary gland; st, stomach; t, testes; vL, valve of Leiblein.

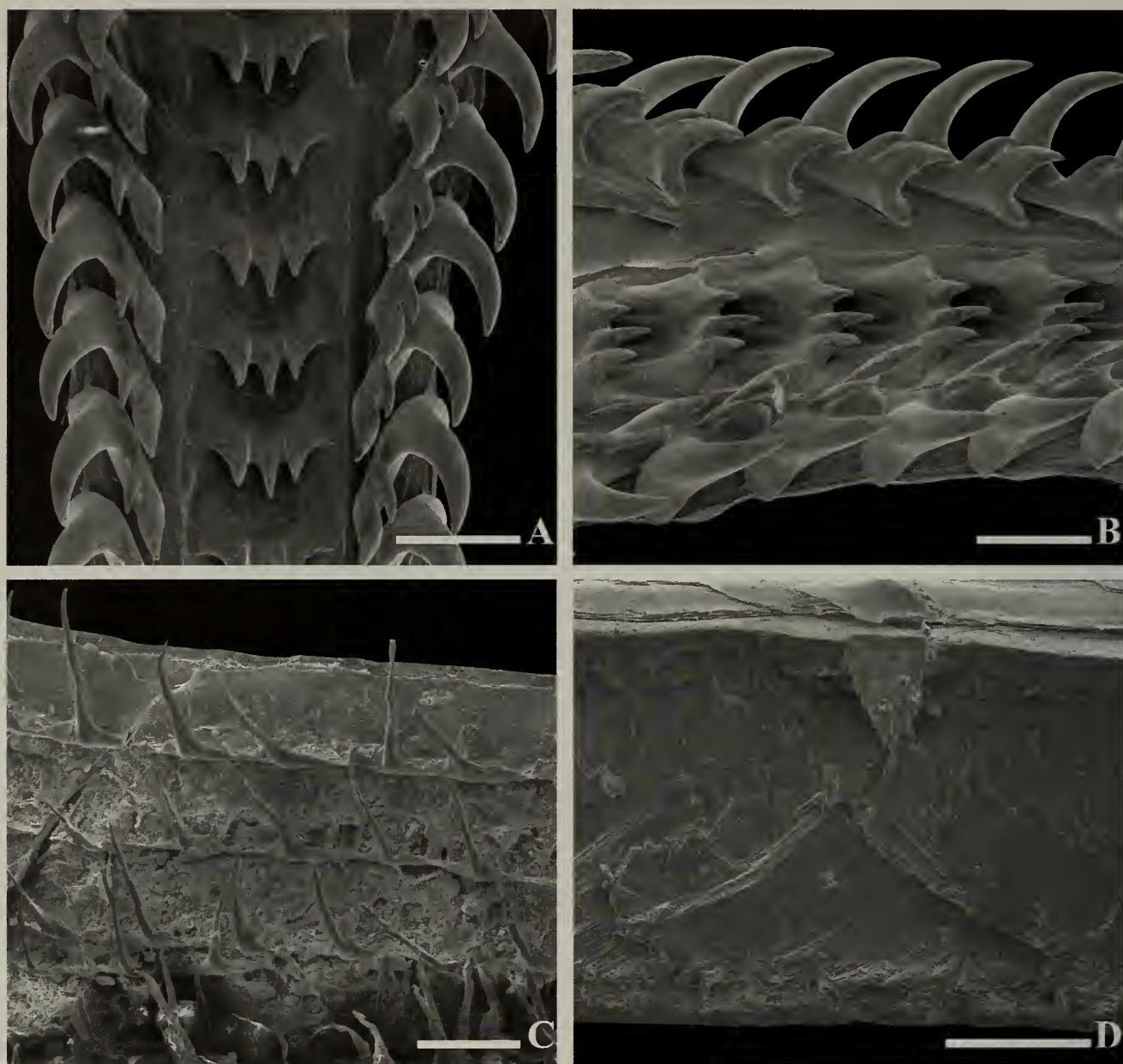


Fig. 6. *Chlanidota* (*Chlanidota*) *densesculpta* (Martens, 1875). A. Dorsal, and B. left lateral (45°) views of the central portion of the radular ribbon taken from animal in Fig. 5. C–D. R/V *Eltanin*, Sta. 1533, South Georgia Island, $54^\circ00'S$, $37^\circ27'W$, in 3–6 m, USNM 896097. C. Periostracum. D. Shell ultrastructure, fracture surface parallel to growing edge. Scale bar = $200\ \mu\text{m}$ for A–C, $100\ \mu\text{m}$ for D.

Type material.—Holotype, MNH-U 37478 (fig. 4A–C).

Material examined.—Holotype. R/V *Eltanin*: Sta. 1533, South Georgia Island, $54^\circ00'S$, $37^\circ27'W$, in 3–6 m, 7 Feb 1966, 1 shell, USNM 870722, 6 specimens, USNM 896097. R/V *Islas Orcadas*: Sta. 18, Off South Georgia Island, $54^\circ02'30''S$, $37^\circ39'36''W$, in 60–71 m, 15 May 1975, 4 specimens, USNM 901650; Sta. 19, Off South Georgia Island, $54^\circ01'42''S$, $37^\circ40'00''W$, in 46–70 m, 15 May 1975, 10 specimens, USNM 901651 (anatomical de-

scriptions are based on specimens from this lot); Sta. 20, Off South Georgia Island, $54^\circ00'06''S$, $37^\circ40'36''W$, in 68–80 m, 15 May 1975, 7 specimens, USNM 901652; Sta. 21, Off South Georgia Island, $53^\circ57'30''S$, $37^\circ20'42''W$, in 27–40 m, 16 May 1975, 1 specimen, USNM 901653; Sta. 95, Off South Georgia Island, $54^\circ11'48''S$, $37^\circ41'06''W$, in 68–80 m, 9 Jun 1975, 3 specimens, USNM 901654. R/V *Prof. Siedlecki*, Sta. 81, Off South Georgia Island, $54^\circ43'S$, $35^\circ13'W$, in 300–306 m, 11 Dec 1986, 1 broken shell, USNM 897523.

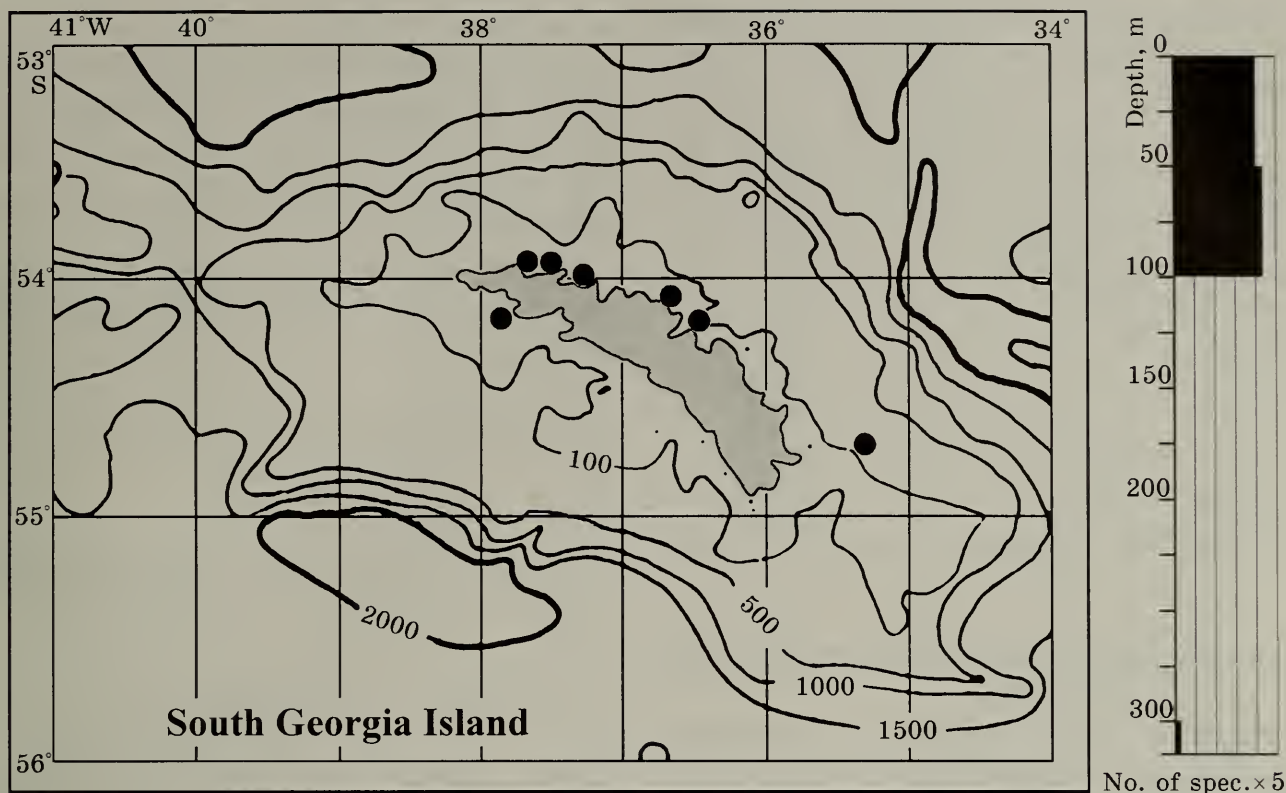


Fig. 7. Geographic distribution and bathymetric range of *Chlanidota (Chlanidota) densesculpta* (Martens, 1875). The type locality is "South Georgia Island."

South Georgia, Bay of Islands, in 7.5 m, 3 specimens, USNM 252874.

Published records.—R/V *Discovery II*: Sta. 45, 2.7 miles S 85°E of Jason Light, South Georgia, in 238–270 m; Sta. 141, East Cumberland Bay, South Georgia, 200 yards from shore under Mt. Duse, in 17–27 m; Sta. 145, Stromness Harbour, South Georgia, between Grass Island and Tonsberg Point, in 26–35 m; Sta. 1941, Leith Harbour, South Georgia, in 55–22 m; Sta. WS 62, Wilson Harbour, South Georgia, in 26–83 m; Sta. MS 6, East Cumberland Bay, ¼ mile south of Hope Point to 1¼ cables S × E of King Edward Point Light, South Georgia, in 24–30 m; Sta. MS 10, East Cumberland Bay, ¼ mile south of Hope Point to ¼ mile south of Government Flagstaff, South Georgia, in 26–18 m (Powell 1951). SW of Snow Hill Island, 64°36'S, 57°42'W, in 125 m (Strebel 1908). Kerguelen (22–345 m) and Crozet (22–505 m) Islands (Cantera & Arnaud 1984).

Distribution.—All of the specimens that we examined were from South Georgia Is-

land. There have been several published reports of *C. densesculpta* occurring at other localities. According to Powell (1951), Martens (1903) record of *C. densesculpta* from Bouvet Island is *Notoficula bouveti* (Thiele, 1912). Strebel (1908:33) neither discussed nor figured the single specimen of *C. densesculpta* he reported from off the Antarctic Peninsula. Similarly, the recent reports of this species from the Kerguelen (22–345 m) and Crozet (22–505 m) Islands (Cantera & Arnaud 1984:68) lack descriptions or illustrations. Pending confirmation of the identification of these records, we provisionally regard *Chlanidota densesculpta* to be endemic to South Georgia Island (Fig. 7). Live-collected specimens were all taken at depths ranging from 3 to 80 m. The only record outside this range is a single dead and broken specimen (R/V *Prof. Siedlecki* Sta. 81) taken in 300–306 m. Dell (1990) misidentified two lots of the bathyal species *Chlanidota (Pfefferia) invenusta* (described below) as *C. (C.) densesculpta*, which led to his incorrect report

Table 4.—*Chlanidota (Chlanidota) pilosa* Powell, 1951. Shell measurements of holotype. Linear measurements in mm.

Character	Holotype
Shell Length (SL)	25.3
Body Whorl Length (BWL)	23.3
Aperture Length (AL)	21.1
Shell Width (SW)	20.0
BWL/SL	0.92
AL/SL	0.83
SW/SL	0.79
No. spiral cords on:	
Penultimate whorl	21
Body whorl	57

of a very broad bathymetric range (0–1400 m) for the latter species.

Remarks.—This species has a striking conchological resemblance to *Chlanidota (Pfefferia) palliata* Strebel, which is also endemic to South Georgia Island, but can be discriminated most easily on the basis of its small operculum (18–0.31 AL, vs. 0.67–0.83 AL in *C. palliata*), which lacks the “feathered” posterior edge diagnostic of

the subgenus *Pfefferia*. *Chlanidota dense-sculpta* is readily distinguished from other species of *Chlanidota* s.s. by its extremely fine and indistinct spiral sculpture as well as by the presence of a thick, finely hirsute periostracum.

Skeletal ossicles of holothurians were found in the rectum of one of the specimens dissected.

Chlanidota (Chlanidota) pilosa
Powell, 1951

Figs. 3, 8; Table 4

Chlanidota pilosa Powell, 1951:139, 194, fig. L73, pl. 8, figs. 29–30; Kaicher 1990: 5807.

Description.—Shell (Fig. 8) small for genus (to 25.5 mm), very thin, translucent, fragile, globose, with very low, rounded spire. Protoconch unknown, early whorls heavily eroded. Teleoconch of evenly rounded, highly convex whorls. Spiral sculpture of numerous fine spiral threads, broader than intervening spaces. Spiral threads sinuated, equal in strength, closely

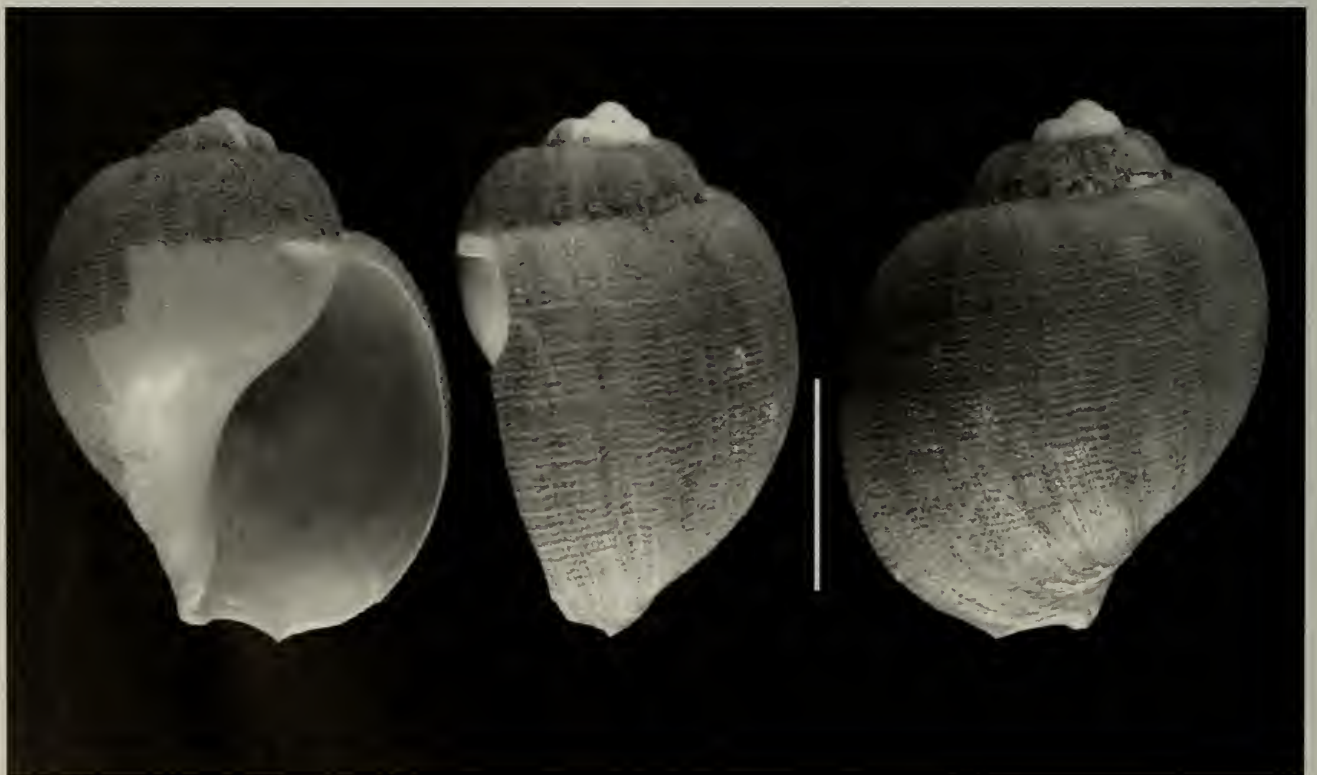


Fig. 8. *Chlanidota (Chlanidota) pilosa* Powell, 1951. Holotype, BMNH 1961500. R/V *Discovery II*, Sta. 456, 1 mile east of Bouvet Island, in 40–45 m. Scale bar = 1 cm.

Table 5.—*Chlanidota (Chlanidota) signeyana* (Powell, 1951). Measurements of shell characters. Linear measurements in mm ($n = 10$, holotype not included).

Character	Mean	σ	Range	Holotype of <i>C. signeyana</i>	Holotype of <i>C. pyriformis</i>	Holotype of <i>C. elongata</i> (from Lamy, 1911)
Shell Length (SL)	29.8	6.7	21.4–42.2	37.4	28.6	30.0
Body Whorl Length (BWL)	24.5	5.1	17.8–33.4	31.9	24.4	26.5
Aperture Length (AL)	19.3	3.5	14.1–25.7	25.3	20.1	20.7
Shell Width (SW)	18.2	3.2	13.5–22.8	23.6	18.6	16.9
Operculum Length (OL)	5.9	1.5	4.5–9.4	6.4	—	—
BWL/SL	0.83	0.02	0.79–0.86	0.86	0.85	0.87
AL/SL	0.65	0.04	0.58–0.70	0.68	0.70	0.69
SW/SL	0.61	0.06	0.54–0.71	0.64	0.65	0.56
OL/AL	0.30	0.04	0.25–0.37	0.27	—	—
No. spiral cords on:						
Penultimate whorl	10.1	2.2	7–14	11	7	7
Body whorl	25.0	6.2	15–35	26	21	21

spaced (2.4–3 per mm), 21 on penultimate whorl, 57 on body whorl. Axial sculpture limited to growth lines. Aperture broadly ovate, deflected from shell axis by 15° . Outer lip very thin, evenly rounded, slightly reflected. Columella $< \frac{1}{2}$ AL, weakly concave, with strong siphonal fold. Callus consisting of a thin glaze overlying parietal region and siphonal fasciole. Siphonal notch broad, slightly dorsally recurved, with straight columellar, rounded apertural margins that mark borders of fasciole without forming raised ridge margins. Shell color white, aperture weakly glazed. Periostracum thin, light yellowish-brown, hirsute. Operculum small (0.3 AL), irregularly ovate. Radula is similar to that *C. (C.) densesculpta* except rachidian cusps are closer together, more broadly triangular, with the central cusp broader and longer than flanking cusps (Dell 1951:fig. L73).

Type locality.—1 mile east of Bouvet Island, in 40–45 m (R/V Discovery II, Sta. 456).

Type material.—Holotype (live collected) BMNH 1961500 (Fig. 8), and paratype (empty shell).

Material examined.—The type material.

Distribution.—Known only from Bouvet Island.

Remarks.—This species is thus far known only from the type material. *Chlanidota pilosa* is similar to low-spired, rotund specimens of *C. densesculpta* (e.g., Fig. 4E), but differs in having fewer and more pronounced spiral riblets on the penultimate and body whorls, and by having a fasciole that lacks a ridge along its margin. These two species are also widely separated in their distribution. *Chlanidota pilosa* differs from *C. vestita* in having a lower spire, as well as more numerous and finer spiral threads.

Chlanidota (Chlanidota) signeyana

Powell, 1951

Figs. 9–11; Table 5

Chlanidota signeyana Powell, 1951:141, fig. F, 194, fig. L74, 196, fig. N129, pl. 8, figs. 34–35; Carcelles, 1953:191, pl. 3, fig. 59; Powell, 1960:150; Kaicher, 1990:5801; Dell, 1990:177, fig. 307.

Cominella (Chlanidota) vestita var. *elongata* Lamy, 1910:319; Lamy, 1911:6, pl. 1 fig. 6.

Chlanidota elongata Powell, 1951:140, 194, fig. L76; Carcelles, 1953:191, pl. 3, fig. 56; Powell, 1960:150; Cernohorsky, 1977:110; Horikoshi et al., 1979: 22, fig.

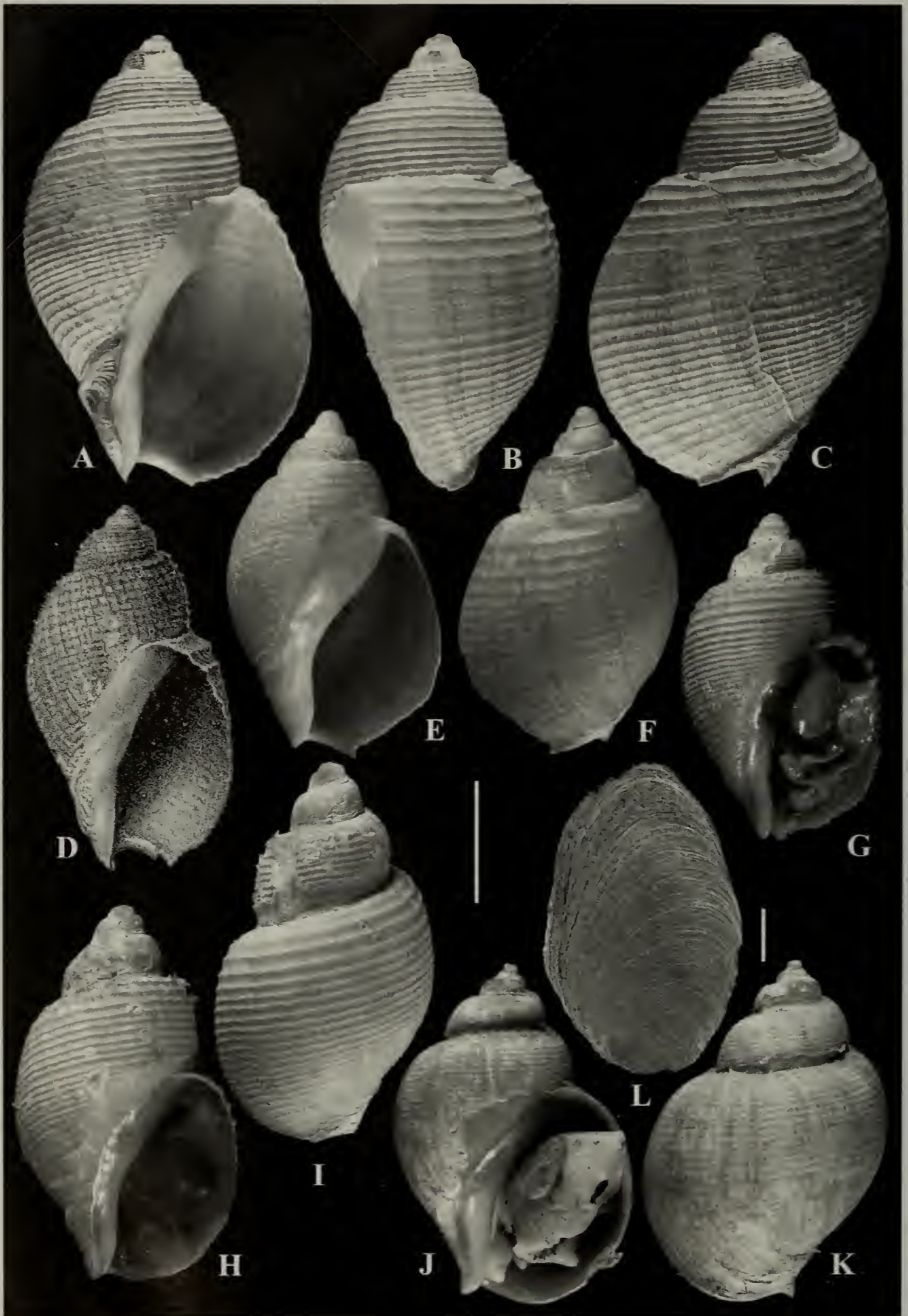


Fig. 9. *Chlanidota* (*Chlanidota*) *signeyana* Powell, 1951. A–C. Holotype, *Chlanidota signeyana*, BMNH 1961512, R/V *Discovery II*, Sta. 167, Off Signy Island, South Orkney Islands, 60°50'30"S, 46°15'00"W, in 244–344 m. D. Holotype, *Cominella* (*Chlanidota*) *vestita* var. *elongata* Lamy, 1910 (from Lamy, 1911), King George Island, South Shetland Islands, in 420 m. E, F. Holotype, *Chlanidota pyriformis* Dell, 1990, USNM 613075,

8; Hain, 1989:71, Taf. V/4, Taf. XXIII/1; Numanami, 1996: 160–162, figs. 106–107.

Chlanidota lamyi Dell, 1990:182, fig. 310, new name for *Cominella* (*Chlanidota*) *elongata* Lamy, 1910, not *Cominella elongata* Dunker, 1857.

Chlanidota pyriformis Dell, 1990:182, fig. 309.

Chlanidota cf. *lamyi* Dell, 1990:182, fig. 315.

Description.—Shell (Fig. 9) large for genus (to 42.6 mm), thin, fragile, elongate to ovate in outline, with medium to high, rounded to turreted spire. Protoconch unknown, early whorls heavily eroded. Teleoconch of up to 5+ evenly-rounded convex whorls, deeply eroded where periostracum damaged or missing. Suture deeply impressed, sharply abutting. Spiral sculpture typically of distinct, sharp, narrow cords (7–14 on penultimate whorl, 15–35 on body whorl) equal or subequal in prominence, that may be reduced or nearly absent in some specimens (Fig. 9F, K). In specimens with pronounced cords (Fig. 9H–I), including the holotype (Fig. 9A–C), 4–5 adapical cords on body and penultimate whorls usually more widely spaced, giving the illusion that they are more pronounced. Spaces between cords equal to cord width on early whorls, at least twice cord width on body whorl. Axial sculpture limited to fine, weakly recurved, prosocline growth lines. Aperture elongate to broadly ovate, deflected from shell axis by 14–17°. Outer lip thin, evenly rounded, fragile. Columella 1/3–1/2 AL, weakly convex, with strong siphonal fold. Callus of thin, silver-edged or thick, brownish glaze overlying parietal region, siphonal fasciole. Siphonal notch broad,

dorsally recurved, with straight columellar and rounded apertural margins that form borders of fasciole. Ridge margin of fasciole extends from apertural margin of siphonal notch. Shell color chalky-white to brownish or orange-tan. Aperture weakly glazed. Periostracum (Fig. 10E) thin to moderately thick, orange-tan to greenish-tan, smooth in weakly sculptured specimens, forming low, axial lamellae with short, hairlike projections on intersections with spiral cords of strongly sculptured specimens. Operculum (Fig. 9L) small (0.25–0.37 AL), broadly ovate, weakly coiled, with terminal nucleus rotated nearly perpendicular to long axis. Operculum may be thin, yellowish, translucent, but usually opaque, brownish to dark brown. Attachment area oval, spanning about $\frac{4}{5}$ of inner surface, posterior and left margins thickened, abraded.

Ultrastructure.—(Fig. 10F) Outermost layer prismatic ($\approx 38 \mu\text{m}$), middle layer comarginal crossed-lamellar ($\approx 60 \mu\text{m}$), inner layer radial crossed-lamellar ($\approx 20 \mu\text{m}$).

Anatomy.—Gross anatomical features of *C. signeyana* very similar to those of *C. densesculpta*, but left and right salivary glands of *C. signeyana* separate, not fused. Radular ribbon long, 9.6–12.2 mm (0.48–0.55 AL), 790–910 μm wide (0.04 AL), triserial (Fig. 10A–D), consisting of 65–75 rows of teeth, posteriormost 5–6 rows nascent. Rachidian teeth with arched base, straight lateral sides, 3 large, robust cusps of equal length. Lateral teeth with 3 cusps, outer cusp longest, intermediate cusp shortest, situated close to inner cusp.

Type locality.—[*Chlanidota signeyana*] Off Signy Island, South Orkneys, 60°50'30"S, 46°15'00"W, in 244–344 m

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R/V *Westwind*, Sta. W-10, off South Shetland Islands, 63°00'S, 60°32'W, in 159 m. G. R/V *Eltanin*, Sta. 997, Gibbs Island, Bransfield Strait, South Shetland Islands, in 769 m, USNM 881971. H–I. R/V *Eltanin*, Sta. 426, Bransfield Strait, South Shetland Islands, in 809–1116 m, USNM 886204. J–K. R/V *Islas Orcadas*, Sta. 55, Saunders Island, South Sandwich Islands, in 64–88 m, USNM 901664. L. Operculum of specimen in figs. J, K. Scale bar = 1 cm for A–K, 1 mm for L.

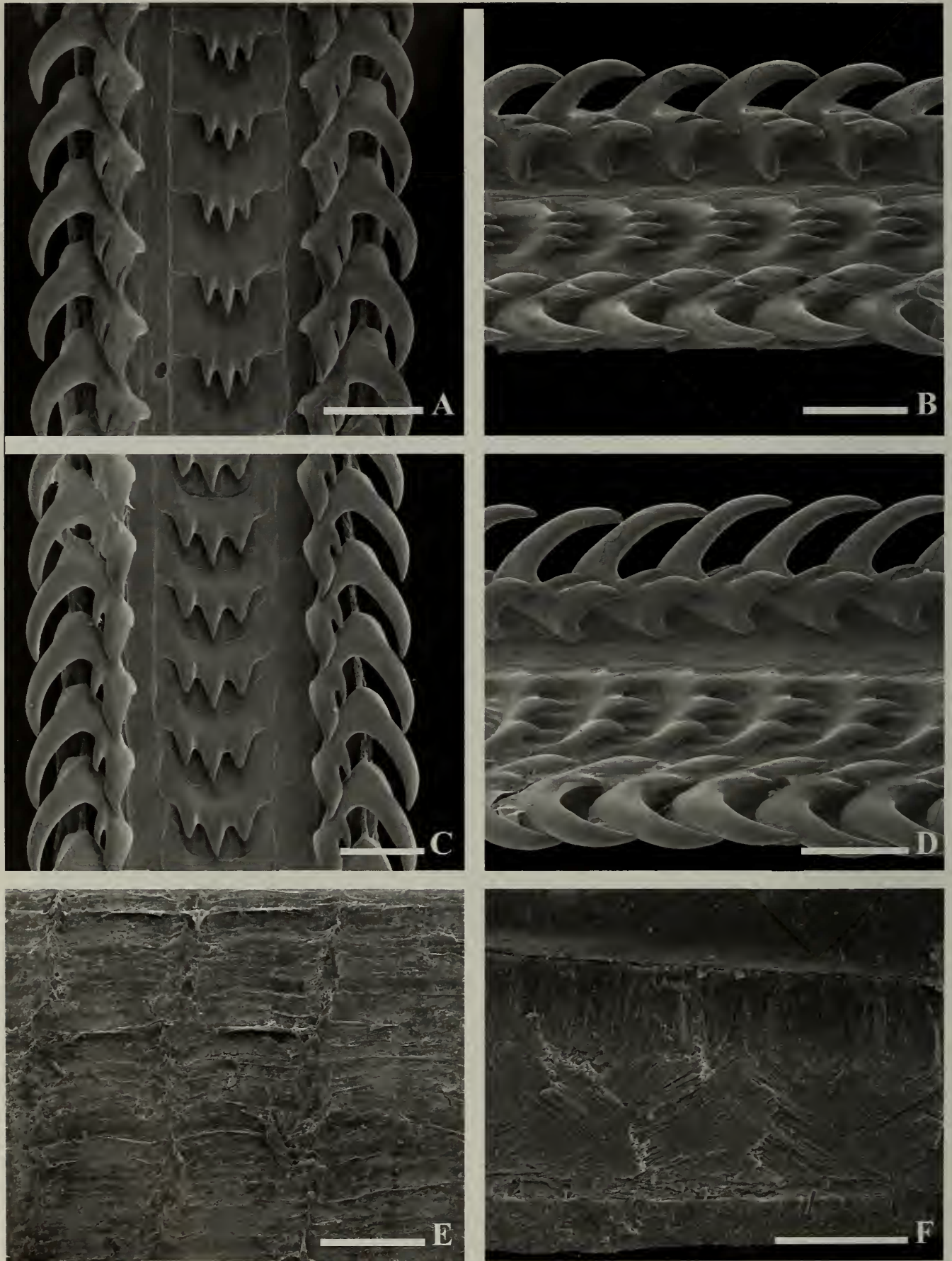


Fig. 10. *Chlanidota* (*Chlanidota*) *signeyana* Powell, 1951. A. Dorsal and B. left lateral (45°) views of the central portion of the radular ribbon taken from the animal in Fig. 9J, K. C. Dorsal and D. left lateral (45°) views of the central portion of the radular ribbon taken from the animal in fig. 9H, I. E. Periostracum and F. shell ultrastructure of the same specimen. Scale bars = 200 μm for A–D, 500 μm for E, 50 μm for F.

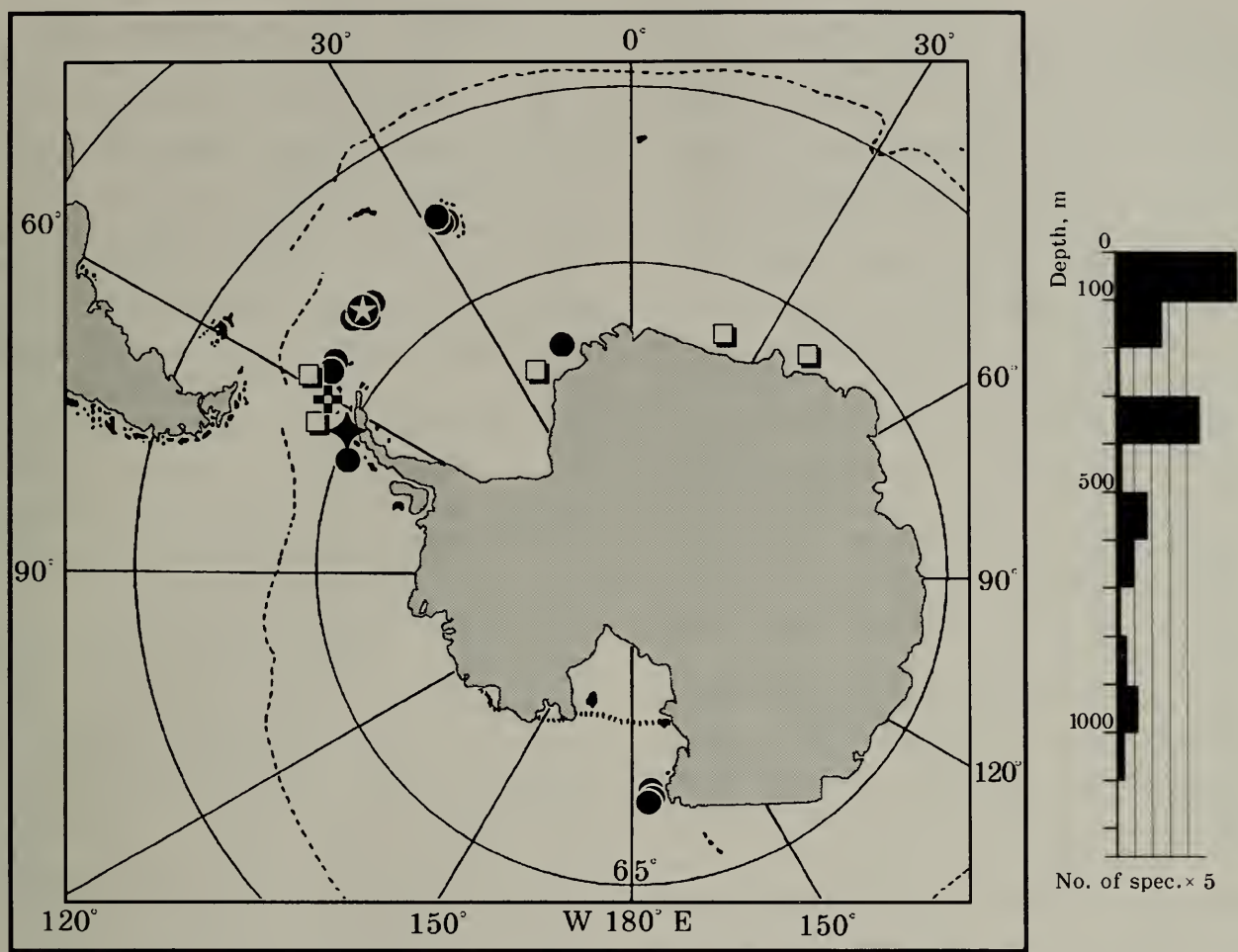


Fig. 11. Geographic distribution and bathymetric range of *Chlanidota* (*Chlanidota*) *signeyana* Powell, 1951. ★ = type locality, *Chlanidota signeyana*; + = type locality, *Chlanidota lamyi*; ◆ = type locality, *Chlanidota pyriformis*. ● = examined material; □ = published records.

(R/V *Discovery II*, Sta. 167); [*Cominella* (*Chlanidota*) *vestita* var. *elongata* Lamy, 1910] King George Island, South Shetlands, in 420 m; [*Chlanidota pyriformis* Dell, 1990] Off South Shetland Islands, 63°00'S, 60°32'W, in 26 m (R/V *Westwind*: Sta. W.10).

Type material.—[*Chlanidota signeyana*] Holotype, BMNH 1961512 (fig. 9A–C), and 2 paratypes; [*Cominella* (*Chlanidota*) *vestita* var. *elongata* Lamy, 1910] The holotype (Fig. 9D) was not found in MNHN; [*Chlanidota pyriformis* Dell, 1990] Holotype, USNM 613075 (Fig. 9E–F) paratypes 1–6, USNM 860181, Paratype 7, MF. 47204.

Material examined.—R/V *Eltanin*: Sta. 426, South Shetland Islands, Bransfield Strait, 62°27'S, 57°58'W, in 809–1116 m, 5 Jan 1963, 3 shell fragments, USNM

870290, 7 shells or fragments, USNM 870291, 4 specimens, USNM 886204; Sta. 428, South Shetland Islands, Bransfield Strait, 62°41'S, 57°51'W, in 662–1120 m, 5 Jan 1963, 1 shell fragment, USNM 870293; Sta. 432, South Shetland Islands, 62°52'S, 59°27'W, in 884–935 m, 7 Jan 1963, fragments of 2 shells, USNM 870303; Sta. 439, Antarctic Peninsula, 63°51'S, 62°38'W, in 128–165 m, 9 Jan 1963, 1 shell, USNM 870313, 1 specimen, USNM 881919; Sta. 444, South Shetland Islands, 62°56'S, 62°02'W, in 750–732 m, 11 Jan 1963, 1 specimen, USNM 881923; Sta. 538, South Orkney Islands, Bransfield Strait, 60°30'S, 47°34'W, in 616–662 m, 6 Mar 1963, fragments of 2 shells, USNM 870330; Sta. 993, South Shetland Islands, Elephant Island, 61°25'S, 56°30'W, in 300 m, 13 Mar 1964, 1 specimen, USNM 881970; Sta. 997,

South Shetland Islands, Bransfield Strait, Gibbs Island, 61°44.18'S, 55°56.06'W, in 769 m, 14 Mar 1964, 1 specimen, USNM 881971; Sta. 1079, Scotia Ridge, 61°26'S, 41°55'W, in 593–598 m, 13 Apr 1964, fragments of 3 shells, USNM 870627, 2 specimens, USNM 881983; Sta. 1084, Scotia Ridge, 60°22'S, 46°50'W, in 298–403 m, 15 Apr 1964, 3 shells, USNM 870641, 7 shells and fragments, USNM 870642, 1 specimen, USNM 881988; Sta. 1997, Ross Sea, 72°00'S, 172°28'E, in 530–549 m, 2 shells, USNM 898205; Sta. 2124, Ross Sea, 71°38'S, 172°00'E, in 606–622 m, 1 shell, USNM 898202; Sta. 2127, Ross Sea, 71°23'S, 171°36'E, in 515–521 m, 1 shell, USNM 898040.

R/V *Eastwind*: Sta. EW66-009, Palmer Peninsula 62°43.1'S, 62°17.5'W, in 561 m, 31 Jan 1966, 1 specimen, USNM 678473; EW66-012, Palmer Peninsula 63°23'S, 60°51'W, in 405 m, 3 Feb 1966, 2 specimens, USNM 678475; EW66-021, off South Orkney Islands, 60°21'S, 45°55'W, in 102 m, 9 Feb 1966, 1 specimen, USNM 678396; EW66-022, off South Orkney Islands, 60°26.5'S, 45°53.3'W, in 168 m, 9 Feb 1966, 1 specimen, USNM 678476; EW66-029, off South Orkney Islands, 61°06'S, 44°57'W, in 290 m, 15 Feb 1966, 1 specimen, USNM 678398; EW66-036, off Elephant Island, 61°16'S, 54°45'W, in 300 m, 17 Feb 1966, 2 shells, USNM 678480; off beach wrack, Collins Pt., Deception Island, 4 Jan 1966, 4 specimens, USNM 678378.

R/V *Hero*: Cruise 691, Sta. 23, off Antarctic Peninsula, Palmer Archipelago, Brabant Island, 64°12.06'S, 62°39.36'W, in 93–95 m, 9 Feb 1969, 1 specimen, USNM 896260; Cruise 691, Sta. 31, South Shetland Islands, Deception Island, 62°58.25'S, 60°45.40'W, in 37–51 m, 13 Feb 1969, 7 specimens, USNM 897557; Cruise 721, Sta. 751, off Antarctic Peninsula, 64°46'28"S, 64°04'20"W, in 33 m, 31 Dec 1971, 1 shell, USNM 901659; Cruise 721, Sta. 765, off Antarctic Peninsula, 64°47.3'S 64°07.4'W, in 55 m, 3 Jan 1972, 1 shell,

USNM 901671; Cruise 721, Sta. 1058, off Antarctic Peninsula, 62°19.0'S, 59°11.4'W, in 44 m, 19 Dec 1971, 1 shell, USNM 901657; Cruise 731, Sta. 1806, 64°46'31"S, 64°04'52"W, in 47–75 m, 18 Feb 1973, 1 specimen, USNM 901686; Cruise 824, Sta. 32-1, Antarctic Peninsula, Anversa Island, 64°37'S, 62°50.48'W, in 640–670 m, 23 Mar 1982, 1 shell, USNM 881583; Cruise 824, Sta. 7-1, Antarctic Peninsula, Adelaide Island, 66°40.40'S, 67°31.23'W, in 510–730 m, 17 Mar 1982, 1 specimen, USNM 896309; Sta. 32-1, Antarctic Peninsula, 64°37'S, 62°50.80'W, in 640–670 m, 25 Mar 1982, 1 shell, USNM 901658.

R/V *Islas Orcadas*: Sta. 39, South Sandwich Islands, 57°01.2'S, 26°44.3'W, in 97–100 m, 23 May 1975, 1 shell, USNM 901663; Sta. 40, South Sandwich Islands, Kadlemas Island, 57°06.8'S, 26°43.36'W, in 15–33 m, 23 May 1975, 1 specimen, USNM 901660; Sta. 42, South Sandwich Islands, Kadlemas Island, 57°06.8'S, 26°43.6'W, in 22–44 m, 24 May 1975, 12 specimens, USNM 901669; Sta. 46, South Sandwich Islands, Kadlemas Island, 57°06.2'S, 26°44.5'W, in 26–60 m, 25 May 1975, 2 specimens, USNM 901665; Sta. 48, South Sandwich Islands, Kadlemas Island, 57°06.3'S, 26°44.2'W, in 27–62 m, 23 May 1975, 4 specimens, USNM 901670; Sta. 55, South Sandwich Islands, Saunders Island, 57°47.12'S, 26°22.30'W, in 64–88 m, 27 May 1975, 1 specimen, USNM 901664; Sta. 57, South Sandwich Islands, 27 May 1975, 5 specimens, USNM 901656; Sta. 80, South Sandwich Islands, Zavodovski Island, 56°20.0'S, 27°38.8'W, in 351–393 m, 4 Jun 1975, 13 specimens, USNM 901667; Sta. 110, Inaccessible Island, 60°28.1'S, 46°27.2'W, in 115–132 m, 16 Feb 1976, 2 specimens, USNM 901666; Sta. 115, Inaccessible Island, 60°32.4'S, 47°22.7'W, in 567–671 m, 17 Feb 1976, 2 shells, USNM 901655; Sta. 118, off South Orkney Islands, 62°01.5'S, 43°06.2'W, in 759–857 m, 20 Feb 1976, 1 specimen, USNM 901661; Sta. 121, off South Orkney Islands, 61°47.00'S,

43°40.00'W, in 616–642 m, 21 Feb 1976, 1 specimen, USNM 901662.

R/V *Westwind*: Sta. W-10, off South Shetland Islands, 63°00'S, 60°32'W, in 159 m, 26 Jan 1958, 6 shells, paratypes of *C. pyriformis* Dell, 1991. USNM 860181, 4 shells, USNM 890897.

R/V *Polar Duke*: off Palmer Peninsula, 65°36'S, 67°21'W, in 200 m, 6 Sep 1985, 1 shell, USNM 846179.

R/V *Deepfreeze IV*: Sta. TD2-ED 14, off Cape Norwegia, Weddel Sea, 71°50'S, 15°50'W, 1028–1122 m, 18 Jan 1959, 1 shell and fragments, USNM 638862.

Published records.—R/V *Discovery II*, Sta. 162, Off Signy Island, South Orkneys 60°48'00"S, 46°08'00"W, in 320 m; Sta. 170, off Cape Bowles, Clarence Is., 61°25'30"S, 60°28'00"W, in 342 m; Sta. 175, Bransfield Strait, South Shetlands, 63°17'20"S, 59°48'15"W, in 200 m; Sta. 1952, between Penguin Island and Lion's Rump, King George I, South Shetlands, in 367–383 m; Sta. 1957, off south side of Clarence Island, South Shetlands, in 785–810 m (Powell, 1951). R/V *Eltanin*: Sta. 426, off South Shetland Islands, 62°27'S, 57°58'W, in 1116–809 m; Sta. 439, west of Antarctic Peninsula, 63°51'S, 62°38'W, in 128–165 m; Sta. 1084, north of South Orkney Islands, 60°22'S, 46°50'W, in 298–403 m, R/V *Hero*: Sta. 23, Antarctic Peninsula, 64°12.1'S, 62°39.6'W, in 93–95 m; Arthur Harbor, Anvers Island, Antarctic Peninsula, 30 m (Dell, 1990:180). PS ANT III/3: Sta. 345, Weddel Sea, 73°27'S, 21°37'W, in 617 m (Hain, 1989). Syowa Sta., Enderby Land, in 98 m (Horikoshi et al., 1979). JARE Sta. 9, Breid Bay, Queen Maud Land, 70°13.7'S, 24°25.7'E, in 276–289 m, Sta. 10, 25 (Numanami, 1996); NZOI: Sta. A463, 72°20'S, 174°50'E, in 460 m; Sta. A464, 72°20'S, 174°00'E, in 376 m (Dell, 1990, as *C. cf. lamyi*).

Distribution.—South Orkneys, South Shetlands, Antarctic Peninsula, and Queen Maud Land, and the eastern margins of the Ross Sea. Living specimens were taken in 30–1116 m (Fig. 11).

We include records for this species reported from the area of Queen Maud Land (as *C. elongata*). Figured specimens from this region (Numanami, 1996:fig. 106A–B, E–F). appear to have weaker, more numerous spiral cords. One specimen from Syowa station has rachidian teeth with narrower cusps and additional serrations, features that had not previously been observed in specimens of *C. signeyana*. Powell (1951:142, fig. L78) reported and illustrated similar additional serrations in a specimen of *Chlanidota (Pfefferia) elata*.

We have examined and also include records from the eastern margin of the Ross Sea, which had been listed as *Chlanidota cf. lamyi* by Dell (1990:310). Dell (1990) noted that these broken and worn specimens closely resemble *C. signeyana* (as *C. lamyi*) from the South Shetland Islands, but differed only in having more numerous spiral cords on their body whorl.

Remarks.—Lamy (1910) was the first to recognize this species, proposing the taxon *Cominella (Chlanidota) vestita* var. *elongata*, without realizing that the name was preoccupied by *Cominella elongata* Dunker, 1857. Powell (1951:141) considered *Chlanidota elongata* to be restricted to the South Shetland Islands and erected the taxon *C. signeyana* based on material from the South Orkney Islands. He recognized that *C. signeyana* was closely related to *C. elongata*, but distinguished it as being “constantly broader and of ovate rather than cylindrical outline.” Cernohorsky (1977:110) noted that *Cominella (Chlanidota) vestita* var. *elongata* Lamy, 1910 was preoccupied, but questioned whether this taxon was distinct from *C. vestita*. After examining a broader range of specimens than were available to Powell, Dell (1990:180) noted that both ovate and cylindrical phenotypes co-occurred in South Shetland and South Orkney samples, but that specimens could be sorted into one or the other phenotype on the basis of the ratio of shell width (SW) to shell height (SH). He regarded *Chlanidota signeyana* to be limited to the ovate

Table 6.—*Chlanidota* (*Chlanidota*) *paucispiralis* Powell, 1951. Measurements of shell characters. Linear measurements in mm ($n = 10$, holotype not included).

Character	Mean	σ	Range	Holotype
Shell Length (SL)	29.8	3.0	21.9–31.7	21.9
Body Whorl Length (BWL)	25.2	2.4	19.2–27.2	19.2
Aperture Length (AL)	19.9	1.8	15.8–21.9	15.8
Shell Width (SW)	19.5	2.1	14.4–21.7	14.4
Operculum length (OL)	4.5	0.7	4.0–5.0	4.0
BWL/SL	0.85	0.01	0.84–0.88	0.88
AL/SL	0.67	0.03	0.63–0.72	0.72
SW/SL	0.65	0.02	0.62–0.68	0.66
OL/AL	0.27	0.02	0.25–0.28	0.25
No. spiral cords on:				
Penultimate whorl	4.4	0.5	4–5	4
Body whorl	10.6	1.6	8–13	10

phenotype with SW/SH ratios ranging from 0.60 to 0.66 and proposed the new name *Chlanidota lamyi* (for *Cominella elongata* Lamy, 1910, non Dunker, 1857) for the elongate phenotype, with SW/SH ratios between 0.55 and 0.60. He did, however, recognize the possibility that “these two forms are but extremes of the same species.”

Dell (1990) also described *C. pyriformis* based on a single lot (11 specimens) collected off the South Shetland Islands, which he regarded to be a morphologically consistent shallow-water form allied to both *C. signeyana* and *C. lamyi*, but distinguished by its tapering, conical spire.

We examined and measured a large series of specimens from throughout the ranges of the three nominal species, but were unable to differentiate between them in any reproducible manner. Larger samples from several stations (e.g., USNM 901669, USNM 897557, USNM 860181) revealed that each population spans the range of morphologies of at least two, and sometimes all three of these nominal species. *Chlanidota signeyana* is highly variable in shell outline and spiral sculpture, and encompasses the phenotypes of *Chlanidota lamyi* and *C. pyriformis*.

There does appear to be a clinal gradient in shell shape, with northern specimens tending to be more inflated, while populations from the southern portion of the spe-

cies' range, including the Antarctic mainland, have a higher proportion of narrower and more cylindrical shells. Numanami (1996:146) recognized a similar gradient in shell morphology in the taxon *Neobuccinum eatoni*, noting that specimens from the Kerguelen and South Shetland Islands tended to be more elongated, while the samples from Enderby Land tended to be more inflated and shorter spired. However, his large sample ($n = 98$) from Enderby Land showed a wide variability in shell form, and included examples from the entire range of variation for the species.

Chlanidota signeyana is most similar to *C. (C.) paucispiralis* Powell, 1951, but differs in having more numerous and weaker spiral cords. Moreover, *C. (C.) signeyana* has not been recorded off South Georgia, while *C. (C.) paucispiralis* is endemic to South Georgia Island.

Chlanidota (*Chlanidota*) *paucispiralis*
Powell, 1951

Figs. 12, 13, 14, 15; Table 6

Chlanidota paucispiralis Powell, 1951:141, 194, fig. L77, pl. 8, figs. 36–37; Carcelles, 1953:191, pl. 3, fig. 57; Powell, 1960:150; Kaicher, 1990:5806; Dell, 1990:183–4, fig. 308.

Description—Shell (Fig. 12) large for genus (to 40.3 mm), thin, strong, ovate to

elongate-ovate in outline, with moderately high, conical spire. Protoconch unknown, early whorls heavily eroded. Teleoconch of up to 5½ evenly-rounded convex whorls. Suture strongly impressed, forming very narrow channel between adapical spiral cord and previous whorl. Spiral sculpture of narrow, sharp, widely spaced cords, 4–5 on penultimate whorl, 8–13 on body whorl. Space between cords wide, evenly concave, with 0–8 very fine spiral threads. Two adapical cords form narrowly tabulate shoulder. Axial sculpture of fine, closely spaced growth lines. Aperture ovate, deflected from shell axis by 9–15°. Outer lip thin, evenly rounded, with serrated edge formed by spiral cords. Columella <½ AL, weakly concave, with pronounced siphonal fold. Parietal callus narrow, thick, overlying spiral cords. Siphonal notch dorsally recurved, with straight columellar, rounded apertural margins that define limits of fasciole. Apertural margin of siphonal notch dorsally deflected, giving rise to low, sharp keel that forms “ridge margin” of fasciole. Shell color chalky white, aperture thinly glazed, occasionally with margins of glaze discolored to gray or golden tan. Periostracum (Fig. 13C, D) thin, smooth, yellowish-tan, sometimes consisting of closely adjacent, blade-like lamellae, which overlay spiral sculpture without giving rise to hair-like projections. Operculum (Fig. 12J) small (0.25–0.28 × AL), broadly ovate, weakly coiled, with laterally terminal nucleus (usually abraded) rotated nearly perpendicular to long axis. Attachment area nearly circular, spanning ⅔ of inner surface, posterior and left margins thickened, glazed.

Ultrastructure.—(Fig. 13D) Outermost layer prismatic (≈90 μm), middle layer comarginal crossed-lamellar (≈235 μm), inner layer radial crossed-lamellar (≈55 μm).

Anatomical features of *C. (C.) paucispinalis* are very similar to those of *C. (C.) densesculpta*. Only a single female specimen

(SL = 27.7 mm) was available for dissection.

External anatomy.—Soft tissues comprise ≈3½ whorls. Mantle cavity just over ½ whorl, kidney ¼ whorl, digestive gland 2¼ whorls. Columellar muscle short, broad, attaching to shell at rear of mantle cavity. Foot small, rectangular (L/W ≈ 1.4), with long (0.2 × foot length) medial, ventral pedal gland. Base color yellowish tan, mottled with patches of grayish black on dorsal surfaces of siphon, tentacles, foot. Head small, with thin cylindrical tentacles, large black eyes. Siphon long, free, muscular.

Alimentary system.—Radular ribbon ≈ 9.0 mm long (0.51 AL), 830 μm wide (0.05 AL), triserial (Fig. 13A–B), of ≈70 rows of teeth, of which 5–7 are nascent. Rachidian teeth with arched base, straight lateral sides, 3 large, robust cusps, central cusp slightly longer than lateral cusps. Lateral teeth with 3 cusps, outer cusp longest and, intermediate cusp shortest, adjacent to inner cusp. Anterior foregut very similar to that of its congeners. Stomach (Fig. 14) differs in having very short caecum, which may be homologous to caecum (posterior mixing area) of Buccinidae.

Type locality.—South Georgia, 53°52'30"S, 36°08'00"W, in 160 m (R/V *Discovery II*, Sta. 159).

Type material.—Holotype, BMNH 1961513 (fig. 12A–C), and 2 paratypes, BMNH 1961513.

Material examined.—Holotype. R/V *Islands Orcadas*: Sta. 8, off South Georgia Island, 53°35'48"S, 37°35'12"W, in 254–366 m, 11 May 1975, 1 shell, USNM 881743; Sta. 10, off South Georgia Island, 53°47'48"S, 37°26'42"W, in 165–234 m, 12 May 1975, 1 shell, USNM 881745; Sta. 12, off South Georgia Island, 53°38'12"S, 37°54'42"W, in 130–137 m, 13 May 1975, 4 shells, USNM 881708; Sta. 13, off South Georgia Island, 53°44'12"S, 37°59'30"W, in 128–137 m, 13 May 1975, 5 shells + fragments, USNM 901672; Sta. 14, off South Georgia Island, 53°41'48"S, 37°57'12"W, in 144–150 m, 14 May 1975, 1 shell, USNM

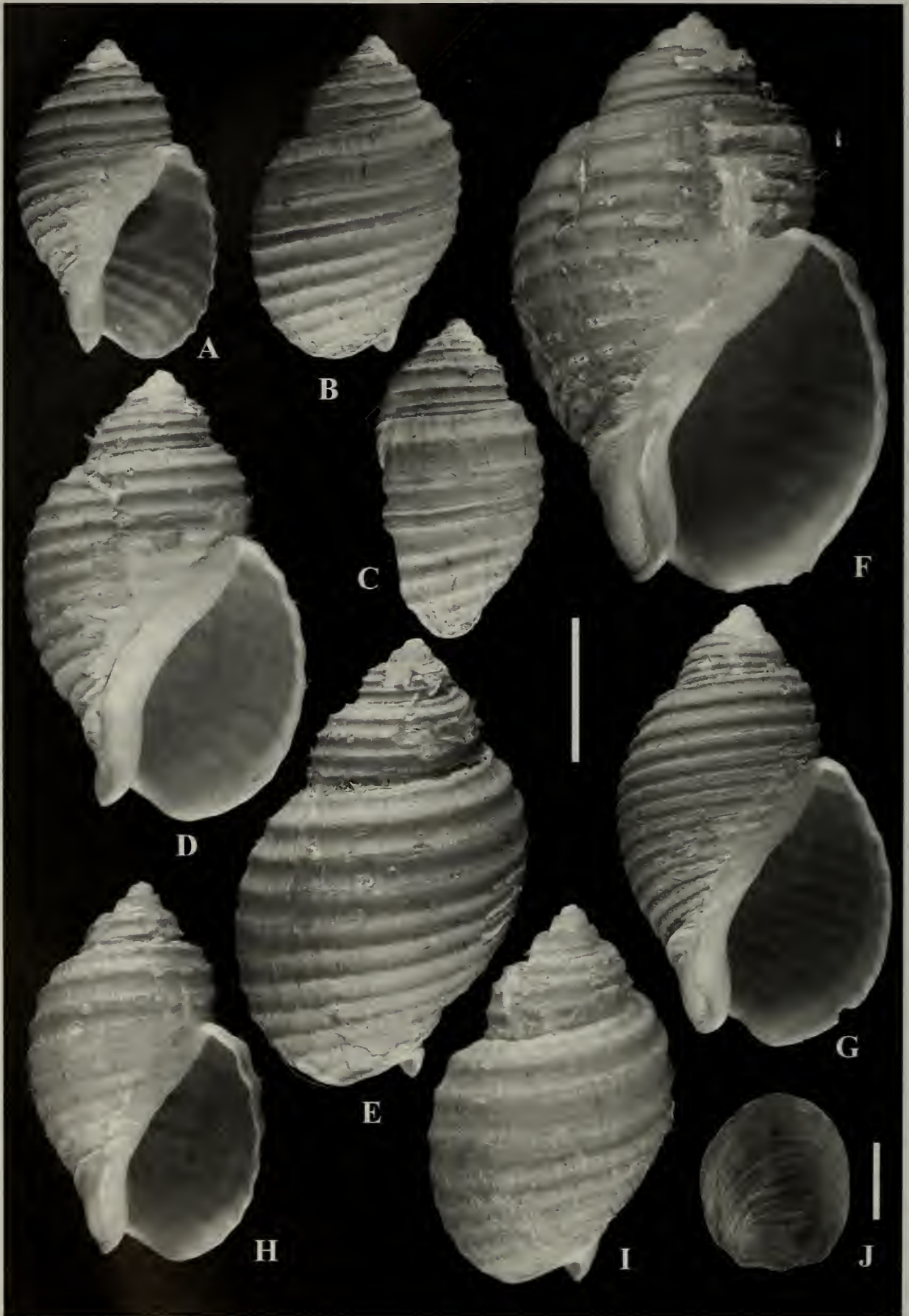


Fig. 12. *Chlanidota (Chlanidota) paucispiralis* Powell, 1951. A–C. Holotype, BMNH 1961513, R/V *Discovery II*, Sta. 159, South Georgia, 53°52'30"S, 36°08'00"W, in 160 m. D, E. R/V *Prof. Siedlacki*, Sta. 105, South Georgia, 53°40'S, 36°48'W, in 161–192 m, USNM 897515. F. R/V *Prof. Siedlacki*, Sta. 20, 53°58'S, 38°42'W, in 189–200 m, USNM 897583. G. R/V *Prof. Siedlacki*, Sta. 16, Off South Georgia Island, 53°44'S,

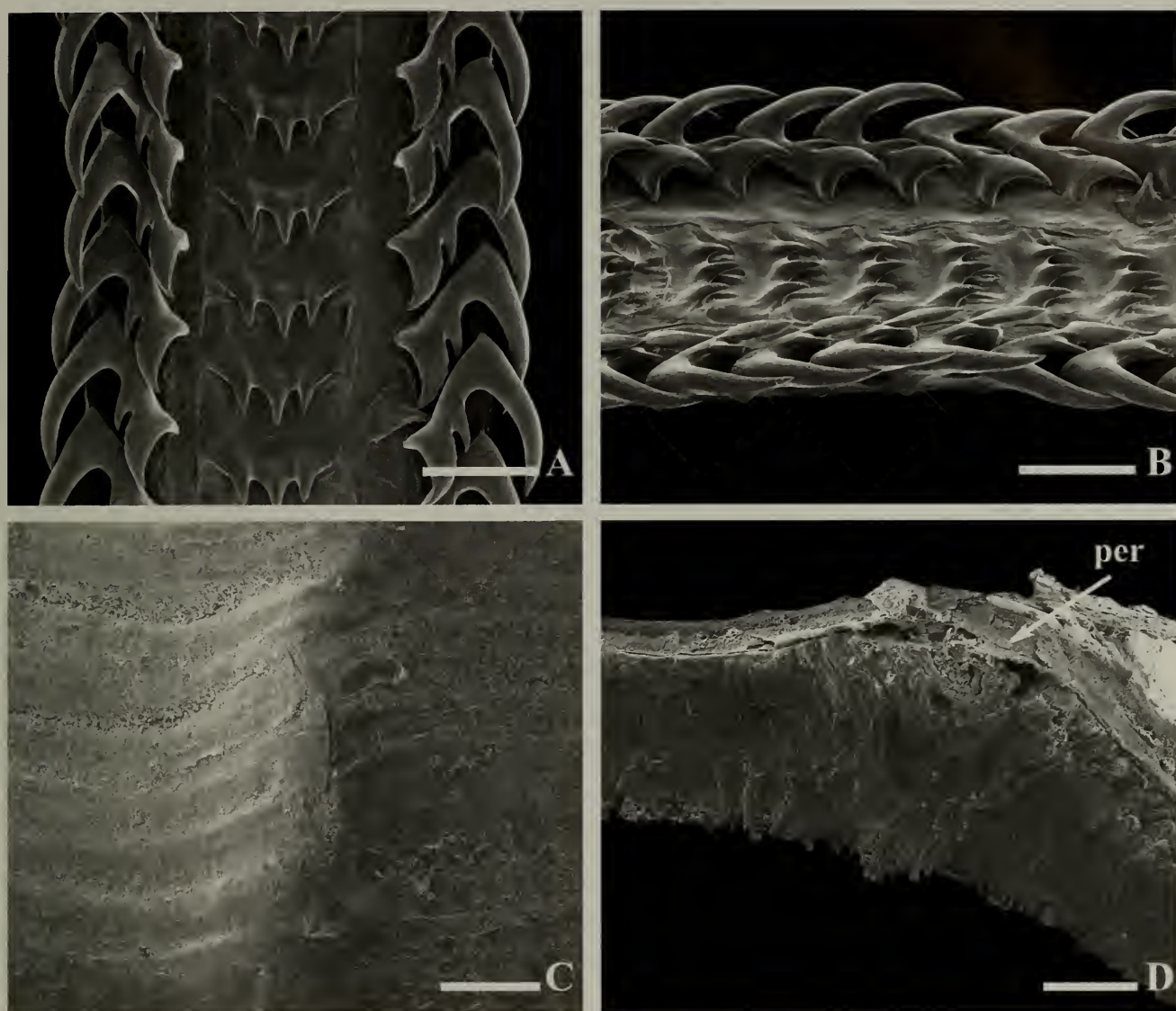


Fig. 13. *Chlanidota (Chlanidota) paucispiralis* Powell, 1951. A. Dorsal and B. left lateral (45°) views of the central portion of the radular ribbon taken from animal in fig. 12H, I. C. Periostracum and D. shell ultrastructure. R/V *Prof. Siedlecki*, Sta. 24, 54°05'S, 38°25'W, in 197–207 m, USNM 897531. Scale bars = 200 μ m.

881716; Sta. 15, off South Georgia Island, 53°37'42"S, 38°04'00"W, in 128–137 m, 14 May 1975, 1 shell, USNM 901673; Sta. 16, off South Georgia Island, 53°38'12"S, 38°01'06"W, in 130–134 m, 14 May 1975, 1 shell, USNM 901675; Sta. 17, off South Georgia Island, 53°36'00"S, 38°03'00"W, in 122–124 m, 14 May 1975, 1 specimen + 2 shells, USNM 901674 (anatomy studied); Sta. 30, off South Georgia Island,

53°50'36"S, 36°18'36"W, in 185–205 m, 19 May 1975, 2 shells, USNM 887839.

R/V *Prof. Siedlecki*: off South Georgia Island, Sta. 16, 53°44'S, 39°22'W, in 304–342 m, 02 Dec 1986, 4 shells, USNM 897553; Sta. 20, 53°58'S, 38°42'W, in 189–200 m, 02 Dec 1986, 2 shells, USNM 897583; Sta. 24, 54°05'S, 38°25'W, in 197–207 m, 03 Dec 1986, 2 shells, USNM 897531; Sta. 28, 54°30'S, 38°56'W, in 220–

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39°22'W, in 304–342 m, USNM 897553. H, I. R/V *Islas Orcadas*, Sta. 17, Off South Georgia Island, 53°36'00"S, 38°03'00"W, in 122–124 m, USNM 901674, (anatomical data based on this E specimen). J. operculum of specimen in figs. H, I. Scale bar = 1 cm for A–I, 2 mm for J.

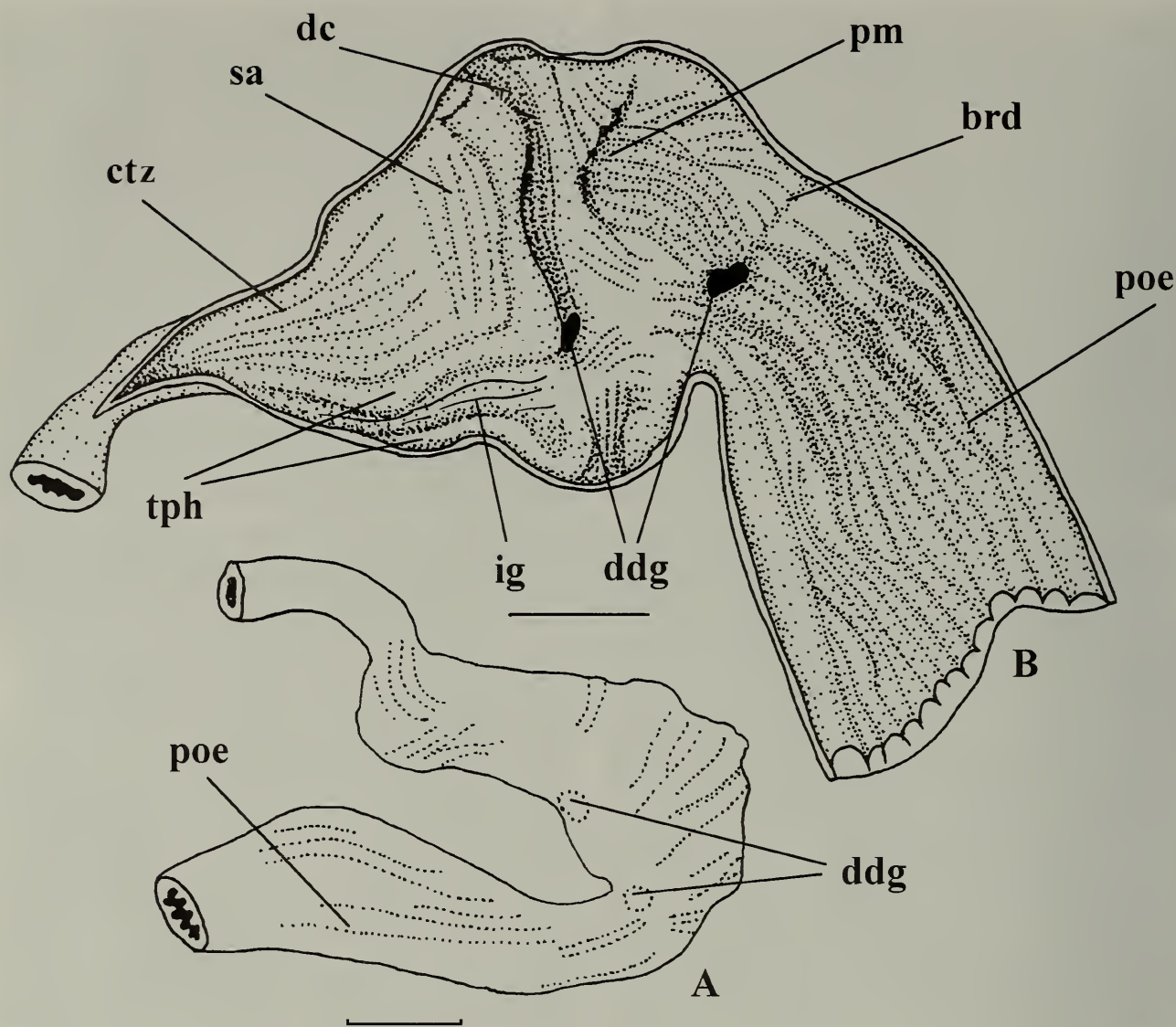


Fig. 14. *Chlanidota (Chlanidota) paucispiralis* Powell, 1951. Stomach of specimen in fig. 12H I. A. Dorsal view of the stomach. B. Stomach opened mid-ventrally. Scale bars = 2 mm. Abbreviations: ctz, compacting zone of the stomach; dc, duct pouch; ddg, duct of the digestive gland; ig, intestinal groove; pm, posterior mixing area, or caecum; poe, posterior oesophagus; sa, sorting area; tph, typhlosoles.

232 m, 03 Dec 1986, 1 shell, USNM 897484; Sta. 87, 54°18'S, 35°37'W, in 238–247 m, 11 Dec 1986, 2 shells, USNM 897537; Sta. 101, 53°47'S, 36°34'W, in 263–277 m, 1 shell, USNM 897457; Sta. 105, 53°40'S, 36°48'W, in 161–192 m, 14 Dec 1986, 1 shell, USNM 897515; Sta. 116, 53°43'S, 38°36'W, in 260–306 m, 16 Dec 1986, 1 shell, USNM 896993; Sta. 121, 53°57'S, 38°10'W, in 90–100 m, 16 Dec 1986, 1 shell, USNM 896991.

R/V *Eltanin*: Sta. 671, off South Georgia Island, 54°41'S, 38°38'W, in 220–320 m, 23 Aug 1963, 1 shell, USNM 870378; Sta. 678, off South Georgia Island, 54°49'S, 38°01'W, in 732–814 m, 24 Aug 1963, 1

juvenile specimen, USNM 881942; Sta. 1535, off South Georgia Island, 53°51'S, 37°38'W, in 97–101 m, 7 Feb 1966, 10 shells + fragments, USNM 898666.

Distribution.—South Georgia Island, in 97–814 m (Fig. 15). Live specimens were collected in 122–814 m.

Remarks.—Unlike most of its congeners, this geographically restricted species displays remarkably little variation in shell morphology. It is readily distinguished from all other *Chlanidota* sensu stricto by its prominent, broadly spaced, spiral cords. It most closely resembles *Chlanidota (Pfefferia) chordata* (Strebel, 1908), from which it is readily distinguished by its small, smooth

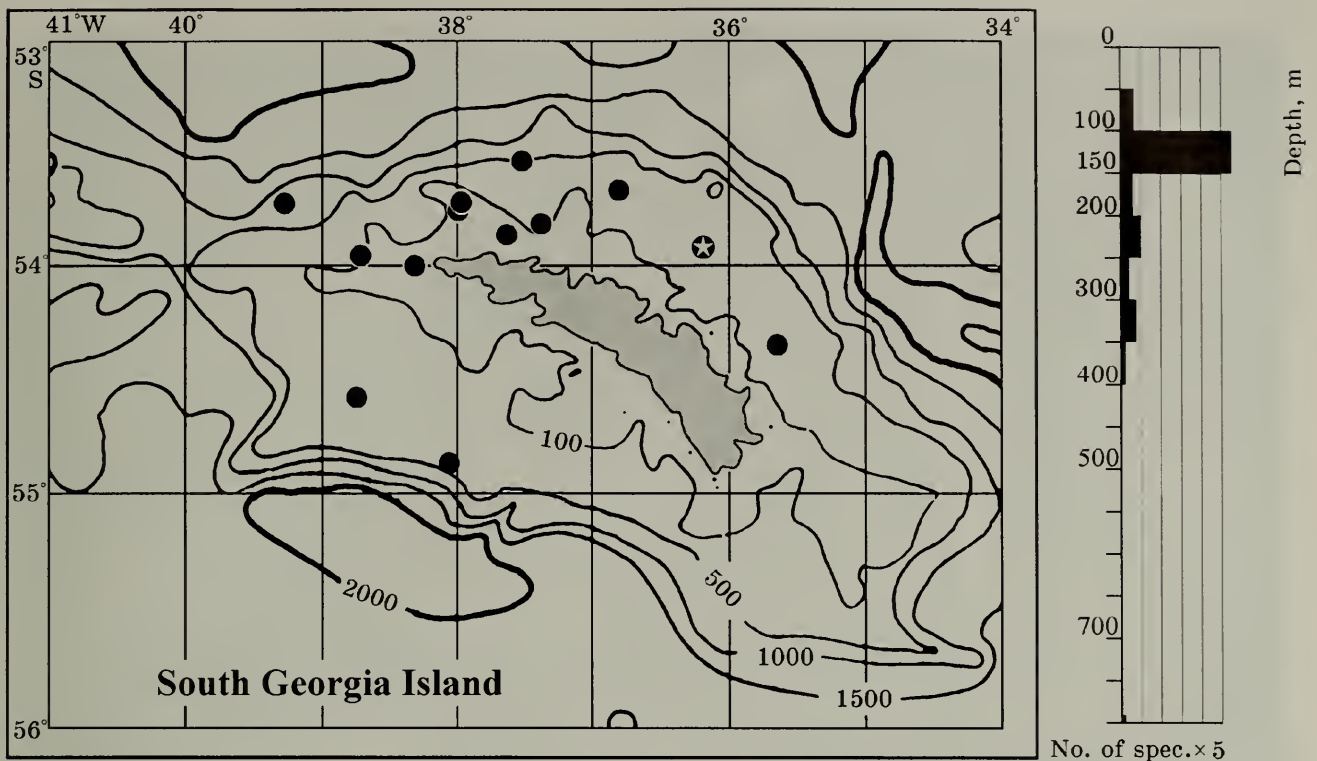


Fig. 15. Geographic distribution and bathymetric range of *Chlanidota* (*Chlanidota*) *paucispiralis* Powell, 1951. ☆ = type locality; ● = examined material.

operculum. *Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908) has a thicker shell and a thicker, hirsute periostracum.

Subgenus *Chlanidota* (*Pfefferia*)
Strebel, 1908

Pfefferia Strebel, 1908:33–4; Powell, 1951:142.

Chlanidota (*Pfefferia*) Thiele, 1929:315.

Type species.—*Pfefferia palliata* Strebel, 1908, by subsequent designation, Powell, 1951:142.

Description.—Shell medium sized for family, maximum adult size 34.5 to 38.3 mm, depending on species. Shell usually moderately thick, ovate to elongate in outline, with short spire. Shell covered with thick periostracum, either smooth or with fine axial lamellae. Spiral sculpture of thin threads or prominent cords. Aperture high, oval. Operculum (Fig. 16) large (0.48–0.83 AL), leaf-shaped, tapered above, below, with terminal nucleus rotated nearly perpendicular to long axis of operculum. Posterior edge of operculum with tall ridge of

feathered lamellae, broadest just above mid-length. Siphonal notch broad, dorsally recurved, siphonal fasciole with ridged margins. Shell ultrastructure and gross anatomy of mantle cavity, alimentary and male reproductive systems as in *Chlanidota* sensu stricto.

Remarks.—The subgenus *Chlanidota* (*Pfefferia*) is endemic to South Georgia Island. In his description of *Pfefferia*, Strebel (1908) noted many similarities with *Chlanidota*, especially in the morphology and sculpture of the shell and periostracum. He distinguished the two as genera on the basis of their opercula, that of *Chlanidota* being small, triangular, with rounded corners, and with its apex and nucleus along the posterior margin. The operculum of *Pfefferia* is much larger, elongated, tapering above and below, and has a characteristic, “feathered” posterior edge. Strebel further commented that low and high-spined forms (without intermediates) were encountered at each of the two stations from which *Pfefferia* had been collected. Each station also contained strongly and weakly sculpture forms. While

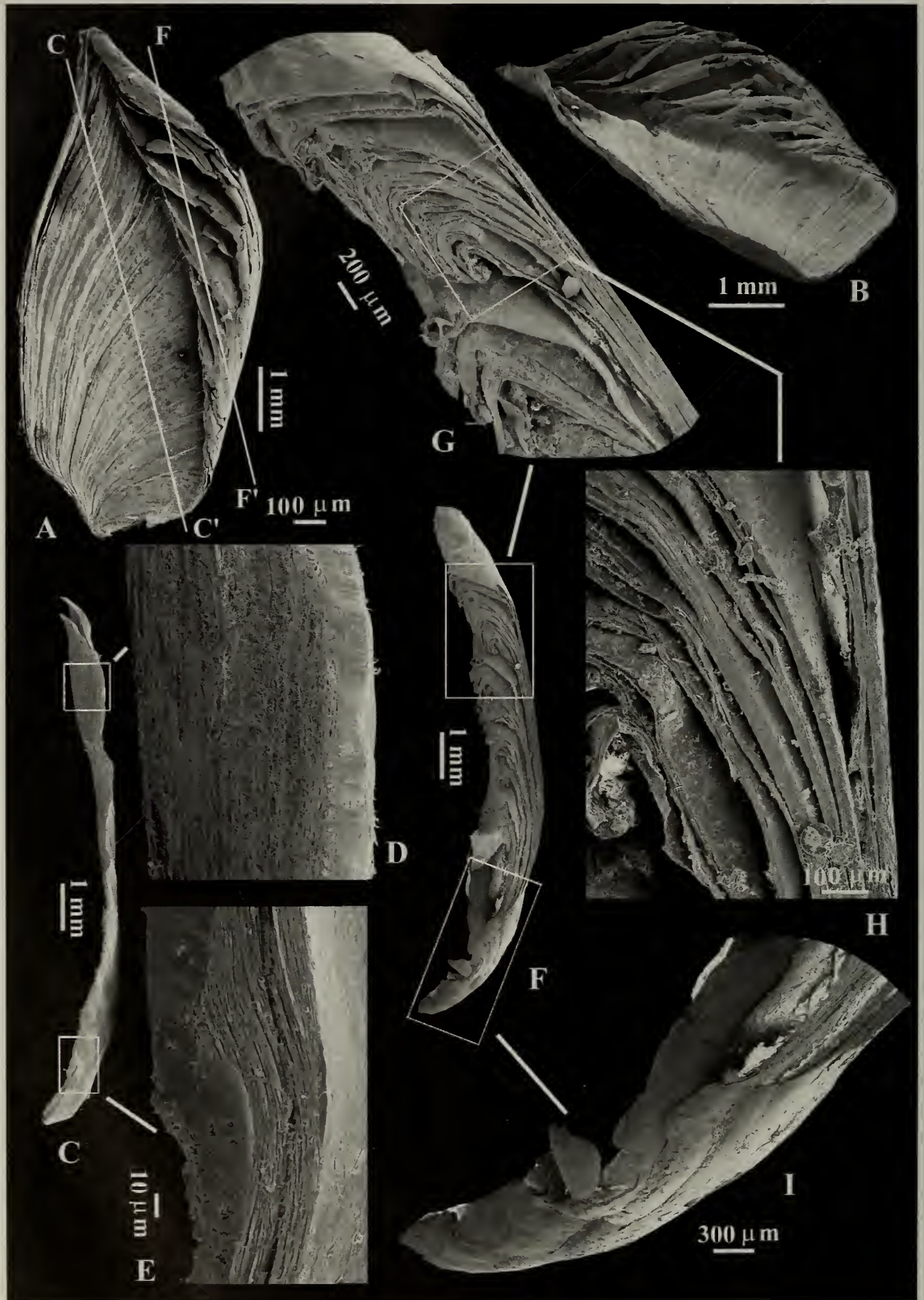


Fig. 16. *Chlanidota (Pfefferia) palliata* (Strebel, 1908). A. Operculum showing terminal nucleus rotated nearly perpendicular to long axis of operculum. Lines C-C' and F-F' correspond to the sections shown by Figs. C and F. B. Left lateral (45°) view of operculum. C. Section trough flat, central portion of operculum (along the line C-C' on Fig. A), nucleus at the bottom. D, E. Successive layers are closely appressed, adherent in this

expressing uncertainty as to whether these differences warranted specific status, Strebel nevertheless described four species, commenting that additional material would allow these questions to be better answered.

Examination and dissection of additional material of three species of *Chlanidota* (*Pfefferia*) revealed that *Chlanidota* (*Pfefferia*) cannot be distinguished from *Chlanidota* sensu stricto on the basis of gross anatomy. Of special interest is the variable operculum of the newly described *C. (P.) invenusta*, which ranges from the typical *Chlanidota* (*Pfefferia*) operculum to one very similar to, but larger than, that of *Chlanidota* (*Chlanidota*), and includes intermediate morphologies. Due to the paucity of distinguishing features, we consider *Chlanidota* (*Pfefferia*) to warrant only subgeneric distinction from *Chlanidota* sensu stricto.

Chlanidota (*Pfefferia*) *palliata*
(Strebel, 1908)

Figs. 17, 18, 19, 20; Table 7

Pfefferia palliata Strebel, 1908:34–5, pl. 3, fig. 39a–f; Thiele, 1912:pl. 16, fig. 20 (radula); Powell, 1951:143; Carcelles, 1953: 193.

Pfefferia elata Strebel, 1908:35, pl. 3, fig. 40; Powell, 1951:142, 194, fig. L78 (radula), 196, fig. N 128 (operculum).

Pfefferia cingulata Strebel, 1908:36, pl. 3, fig. 42a–c; Powell, 1951:142–3, 194, fig. L79 (radula); Carcelles, 1953: 193.

Description.—Shell (Fig. 18) large for genus (to 34.5 mm, Powell, 1951:142), thick, solid, ovate-rounded. Protoconch, early teleoconch whorls eroded in all specimens. Teleoconch with up to 4 evenly inflated whorls. Shoulder not pronounced. Suture deep, adpressed, narrowly chan-

neled. Spiral sculpture of alternating broad, low cords (10–17 on body whorl, 3–5 on penultimate whorl) and fine threads (20–24 per 5 mm), spanning entire shell surface. Cords more clearly visible on young specimens with thinner periostracum. Axial sculpture limited to indistinct growth lines. Aperture tall, ovate, deflected from the shell axis by 16–18°. Siphonal canal is not pronounced. Outer lip evenly rounded, thick, weakly reflected in adults, very thin in juvenile and some adult specimens. Columella <math>< \frac{1}{2}</math> AL, weakly concave, with fine pustules. Siphonal fold strong. Callus thick, clearly demarcated, narrowly overlying parietal region, siphonal fasciole in mature specimens. Siphonal notch broad, dorsally reflected, columellar margin straight, apertural margin rounded, reflected, forming pronounced ridge margin along adapical edge of fasciole. Shell color grayish white, translucent. Periostracum very thick, tightly adherent to shell surface, with evenly spaced, axially reflected lamellae with fringed edges evident on early whorls and juvenile specimens (Fig. 19C). Operculum (Fig. 16A, D) large, leaf-shaped, with apical nucleus, massive, raised, lamellose border along posterior margin, 0.67–0.83 AL. Attachment area spans nearly entire inner surface, posterior, left margins thickened, glazed.

Ultrastructure.—(fig. 19E) Outermost layer prismatic ($\approx 50 \mu\text{m}$), middle layer comarginal crossed-lamellar ($\approx 175 \mu\text{m}$), inner layer radial crossed-lamellar ($\approx 95 \mu\text{m}$). Inner surface of the outer aperture lip with numerous, fine spherules (Fig. 17D).

External anatomy.—Body of 2½ whorls (Fig. 18A, B), mantle cavity spanning $\approx \frac{1}{2}$ whorl, kidney $\frac{1}{5}$ whorl, digestive $1\frac{3}{4}$ whorl. Foot of preserved specimens short (L/W ≈ 1), with rounded posterior edge. Head

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region of the operculum. F. Section through “feathered” portion of operculum (along the line F-F’ on Fig. A), nucleus at the bottom. G, H. Successive layers are unattached along apical portion of posterior edge of operculum. I. new lamellae are deposited along the entire length of the operculum.

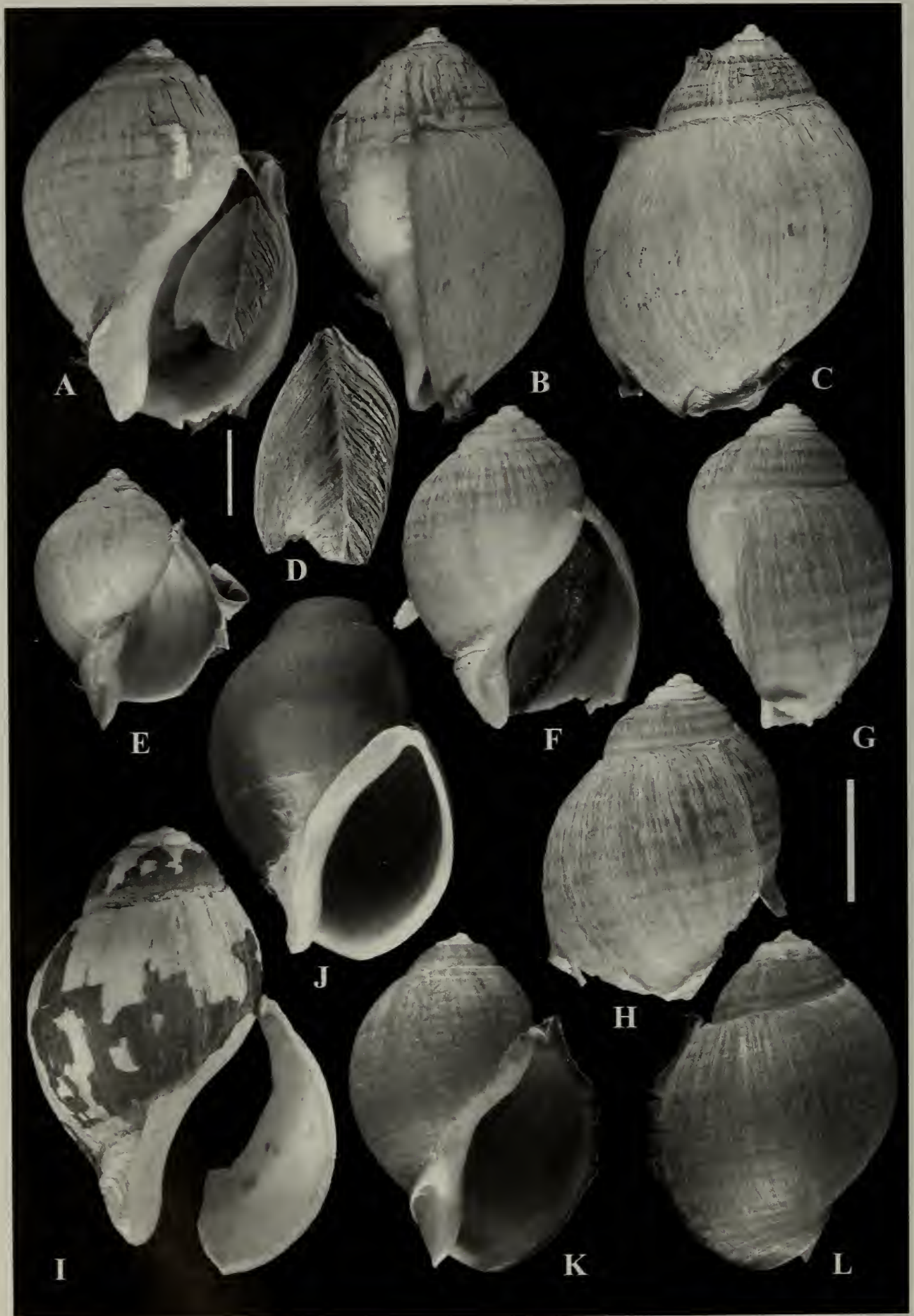


Fig. 17. *Chlanidota (Peffeira) palliata* (Strebel, 1908). A–C. Lectotype, SMNH (here designated), Sveska Südpolarexp., Sta. 22, South Georgia, 54°17'S, 36°28'W, in 75 m. D. Operculum of lectotype, enlarged.

Table 7.—*Chlanidota (Pfefferia) palliata* (Strebel, 1908). Measurements of shell characters. Linear measurements in mm ($n = 10$, type material not included).

Character	Mean	σ	Range	Lectotype of <i>C. palliata</i>	Lectotype of <i>C. cingulata</i>	Holotype of <i>C. elata</i> (broken)
Shell Length (SL)	27.1	3.6	18.1–30.0	32.8	25.9	~37
Body Whorl Length (BWL)	24.6	3.4	16.4–27.1	29.2	23.7	~32
Aperture Length (AL)	19.3	2.0	14.4–20.4	23.5	19.8	~23
Shell Width (SW)	19.4	2.3	14.0–21.2	23.4	19.4	~22
Operculum Length (OL)	14.1	2.0	9.6–16.7	—	15.4	—
BWL/SL	0.91	0.02	0.86–0.95	0.89	0.92	~0.86
AL/SL	0.72	0.04	0.67–0.80	0.72	0.76	~0.62
SW/SL	0.72	0.03	0.68–0.78	0.71	0.75	~0.60
OL/AL	0.73	0.06	0.67–0.83	—	0.78	—

narrow, with stout, conical tentacles, eyes on small lobes. Body lacks pigmentation.

Mantle cavity.—Mantle edge smooth. Siphon medium to long, muscular, extending substantially beyond mantle edge ($\approx \frac{1}{3}$ AL). Osphradium dark greenish-brown, bipectinate, spans $\approx \frac{1}{2}$ mantle length. Hypobranchial gland of few, distinct, widely spaced folds. Ctenidium large, wide, spans $\approx \frac{3}{4}$ mantle length, lamellae tallest in posterior $\frac{1}{4}$ of ctenidium, becoming shorter anteriorly.

Alimentary system.—Proboscis (Fig. 19C, D, pr) thick ($L/D \approx 3.5$), of moderate length (0.9 AL). Mouth opening, triangular slit. Buccal mass muscular, large, nearly equal to retracted proboscis in length. Odontophoral cartilages paired, fused anteriorly, spanning $\approx \frac{2}{3}$ of proboscis length. Radular ribbon (Fig. 18A, B) of moderate length, 10.6 mm (0.66 AL), $\approx 760 \mu\text{m}$ wide (0.05 AL), triserial, consisting of 60–65 rows of teeth, posteriormost 5 nascent. Rachidian teeth with arched base, nearly straight lateral sides, 3 large, robust cusps of equal length. Central cusp longer than flanking cusps in one specimen (Fig. 18A,

B). Lateral teeth with 3 cusps, outer cusp longest, intermediate cusp shortest, adjacent to inner cusp. Intermediate cusp nearly fused to inner cusp in one specimen (fig. 18A, arrow). Salivary glands small, fused (Fig. 19G), situated above nerve ring. Right salivary gland completely covering valve of Leiblein. Salivary ducts run loosely along both sides of oesophagus, entering esophageal wall near posteriormost portion of retracted proboscis. Valve of Leiblein (Fig. 18E, vL) well defined, large, without ciliated cone. Gland of Leiblein (Fig. 18C–E, gL) long, tubular, coiled anteriorly, tapering posteriorly. Oesophagus wide, muscular, expanding posteriorly to form crop (Fig. 18I, poe) lined with tall longitudinal folds. Stomach (Fig. 18H, I) U-shaped, without caecum. Ducts of digestive gland paired, closely spaced, transverse fold slightly raised. Typhlosoles present, poorly defined. Rectum terminating with well defined anal papilla.

Female reproductive system.—Typically buccinoidean. Oviduct opens into medium-sized albumen gland. Ingesting gland single. Capsule gland large, occupies $\approx \frac{1}{2}$ of

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E. Paralectotype, SMNH, from the type locality. F–H. Lectotype of *Pfefferia cingulata* (Strebel, 1908) (here designated), Sveska Südpolarexp., Sta. 34, Cumberland Bay, South Georgia, $54^{\circ}11'S$, $36^{\circ}18'W$, in 252–310 m. I. Holotype of *Pfefferia elata* (broken specimen), same station as types of *C. (P.) palliata*. J, K, L, both from R/V *Islas Orcadas*, Sta. 33, $54^{\circ}30.7'S$, $35^{\circ}35.9'W$, in 261–267 m, USNM 901676. Scale bar = 1 cm for A–C, E–L, 5 mm for D.

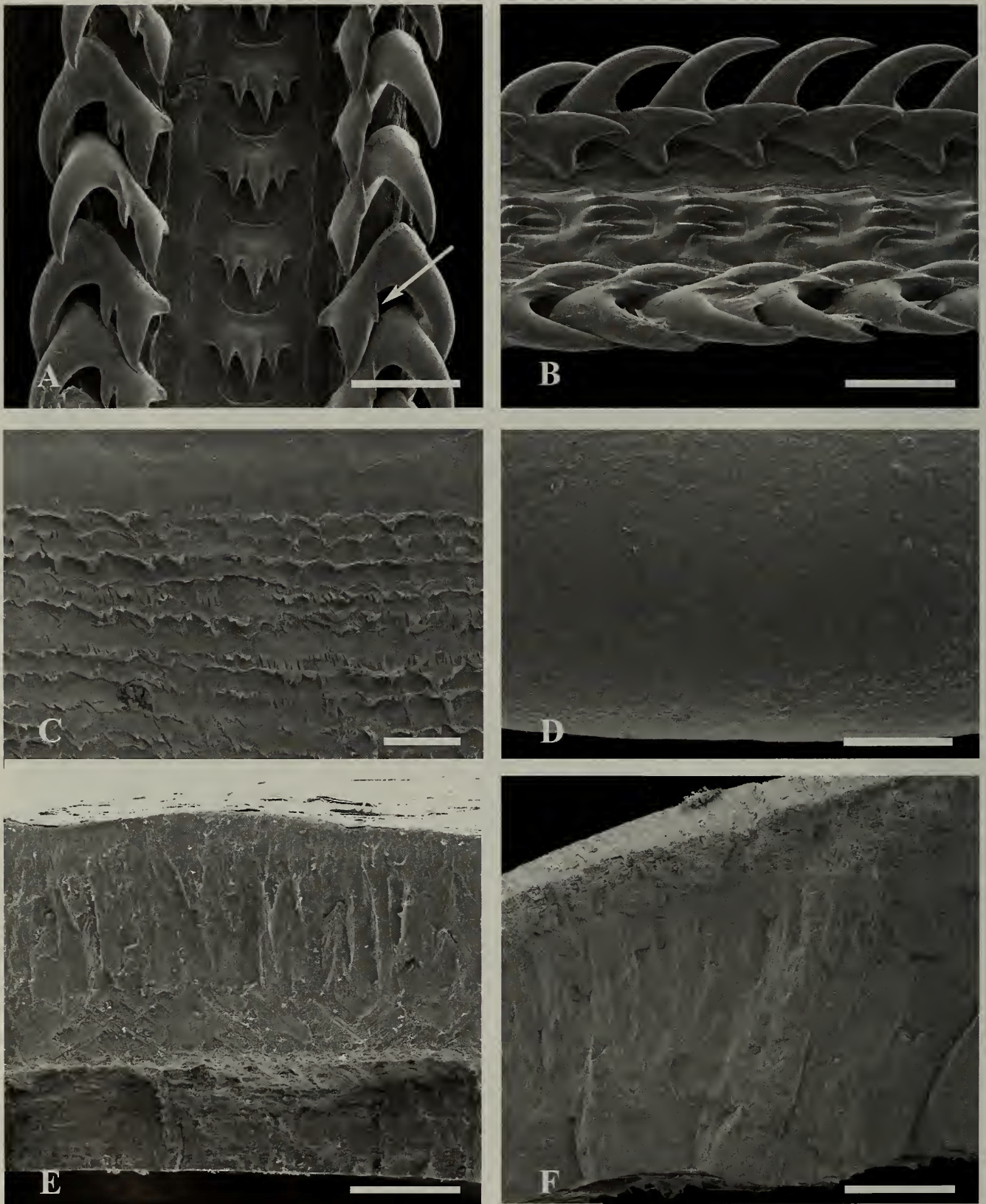


Fig. 18. *Chlanidota (Pfefferia) palliata* (Strebel, 1908). A. Dorsal, and B. left lateral (45°) views of the central portion of the radular ribbon taken from animal in Fig. 17J. C. Periostracum. D. Edge of outer lip. E, F. Shell ultrastructure. E. Fracture surface parallel to outer lip. F. Fracture surface perpendicular to outer lip. Scale bars = 200 μm for A, B, 100 μm for C–F.

mantle cavity. Bursa copulatrix present, simple, hemispherical.

Male reproductive system.—Very similar to that of *C. (C.) densesculpta*, penis has the same size, overall shape, terminal papilla.

Type locality.—[*Pfefferia palliata* & *P. elata*] South Georgia, 54°17'S, 36°28'W, in 75 m (Sveska Südpolarexp., Sta. 22); [*Pfefferia cingulata*] Cumberland Bay, South Georgia, 54°11'S, 36°18'W, in 252–310 m. (Sveska Südpolarexp., Sta. 34).

Type material.—[*Pfefferia palliata*] Lectotype (here designated) SMNH (fig. 17A–C), and 2 paralectotypes SMNH (fig. 17E); [*Pfefferia elata*] Holotype, SMNH 3661 (Fig. 17I), broken specimen; [*Pfefferia cingulata*] Lectotype (here designated) (Fig. 16F–H) and juvenile paralectotype, SMNH.

Material examined.—Type material. R/V *Islas Orcadas*: Sta. 31, 19 May 1975, 54°05.36'S, 36°30.48'W, 130–143 m, 1 shell, USNM 887863; Sta. 32, 19 May 1975, 54°21.36'S, 35°58.42'W, 141–164 m, 1 shell, USNM 887872; 9 shells, USNM 887867; Sta. 33, 19 May 1975, 54°30.7'S, 35°35.9'W, 261–267 m, 27 specimens, USNM 901676.

Published records.—R/V *Discovery II*, Sta. 30, West Cumberland Bay, South Georgia, 2.8 miles S, 24°W of Jason Light [16 Mar 1926], 251 m (Powell, 1951:142).

Distribution.—Known only from off the northeastern coast of South Georgia (Fig. 19). Live material was collected between 75 and 310 m.

Remarks.—The type specimens of *Chlanidota (Pfefferia) palliata* and *C. (P.) elata* were taken from the same dredge haul. Strebel (1908) distinguished these taxa primarily on the difference in their spire height and the strength of their spiral sculpture, but questioned whether these differences merited specific recognition. We were able to examine a larger sample than was available to Strebel (USNM 901676, $n = 27$) and found it to contain specimens spanning a morphological continuum between these two forms. The type series of

C. (P.) cingulata was collected very near the type locality of *C. (P.) palliata*, but at slightly greater depth. The specimen selected as lectotype of *C. (P.) cingulata* is, in our opinion, conspecific with the specimen selected as lectotype of *C. (P.) palliata*, as both fall within the range of morphological variation found in a single population (USNM 901676). Since Powell (1951) designated *P. palliata* to be the type species of *Pfefferia*, we retain this name for this species, and synonymize the remaining nomina.

Powell (1951:142) noted that the only radula he examined was abnormal, with two small, “incipient” cusps flanking the normally tricuspid rachidian teeth. The radulae we examined were typical of *Chlanidota*.

Juvenile specimens are bicolored, with the periostracum being dark chestnut brown above the periphery, and a pale, olive green below the periphery. The periostracum of adult specimens is thicker and uniformly chestnut brown in color. Conchologically this species is similar to *C. (C.) densesculpta*, but may be readily distinguished on by the presence of weakly raised spiral cords, as well as by its distinctive operculum.

Chlanidota (Pfefferia) chordata
(Strebel, 1908)

Figs. 21, 22, 23; Table 8

Pfefferia chordata Strebel, 1908:36–7, pl. 3, fig. 41a–c; Powell, 1951:143; Carcelles, 1953:193.

Description.—Shell (Fig. 20) large for genus (to 35.3 mm), thick, solid, ovate-rounded, highly variable. Protoconch, early teleoconch whorls eroded in all specimens. Teleoconch with up to 4+ evenly rounded, very convex whorls. Shoulder not pronounced. Body whorl comprises 0.6–0.89 of the total shell length. Suture strongly impressed, forming narrow channel between adapical spiral cord and previous whorl. Spiral sculpture variable, spiral cords (7–26 on body whorl, 4–11 on penultimate whorl)

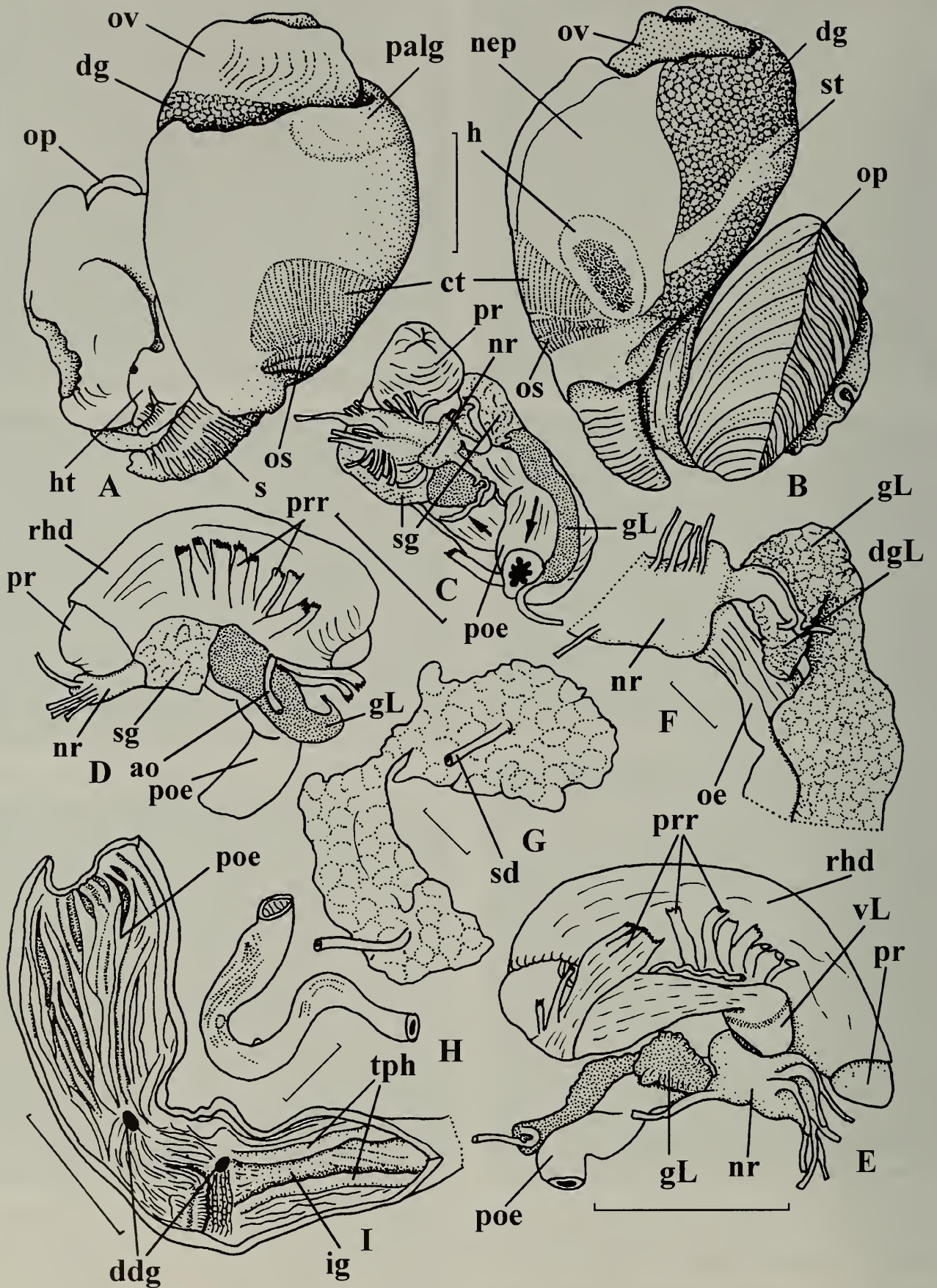


Fig. 19. Anatomy of *Chlanidota (Pfefferia) palliata* (Strebel, 1908). Specimen in fig. 17 J. A. Right and B. left lateral views of animal removed from shell (SL = 29.7 mm). C. Ventral, D. left lateral, and E. right lateral views of anterior alimentary system (salivary glands removed to show valve of Leiblein in E). F. Juncture of gland of Leiblein and esophagus. G. Ventral view of fused salivary glands. H. Dorsal view of stomach. I. Stomach, opened mid-dorsally. Scale bars = 5 mm for A-E, H-I; 2 mm for F, G. Abbreviations: ao, anterior

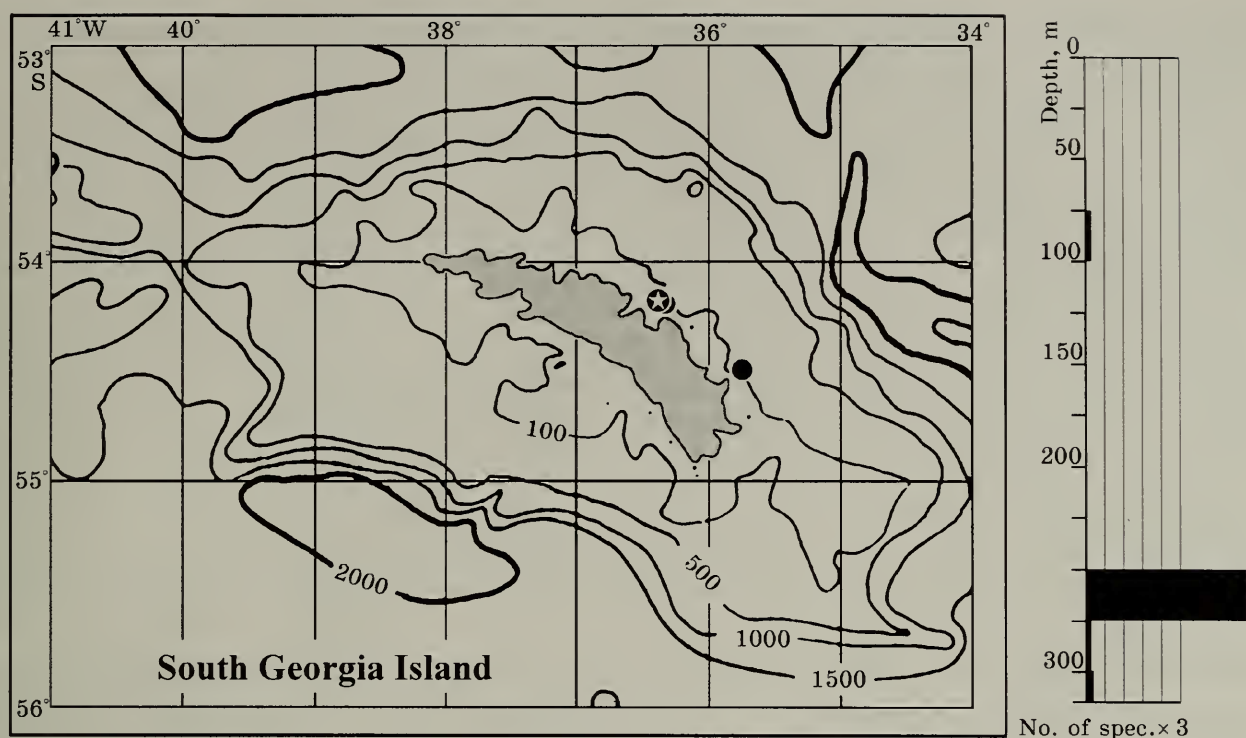


Fig. 20. Geographic distribution and bathymetric range of *Chlanidota (Pfefferia) palliata* (Strebel, 1908). ☆ = type locality; ● = examined material.

low, weak, and smooth to very tall and sharply-defined, forming corresponding spiral grooves on inner surface of outer lip. Cords of weakly sculptured specimens (Fig. 20L, M) closely spaced, as wide or wider than intervening spaces. Cords of moderately sculptured specimens (e.g., Fig. 20A–C, F–G) $\frac{1}{2}$ to $\frac{1}{3}$ width of intervening spaces. Cords of strongly sculptured specimens (Fig. 20D–E, K–J) more than $\frac{1}{2}$ the width of intervening spaces. Adapical cord of strongly corded specimens may form narrowly concave subsutural rim. Fine spiral threads may be present on cords and in interspaces. Axial sculpture limited to weakly defined growth lines. Aperture tall (0.60–0.84 SL), ovate, deflected from shell axis by 16–19°. Outer lip thin to moderately thick, evenly rounded or scalloped, fragile to strong, sometimes slightly reflected. Col-

umella less than half aperture length, weakly convex or straight, with strong siphonal fold. Callus usually thick, narrow, overlying parietal region, siphonal fasciole, grayish to brownish in color. Siphonal notch broad, dorsally recurved, with straight columellar and rounded apertural margins that form borders of fasciole. Ridge margin of fasciole pronounced, originating at apertural margin of siphonal notch, sometimes protruding through callus. Shell color chalky-white. Periostracum (Fig. 21) yellow-orange, olive to dark brown, nearly black, moderately to extremely thick, tightly adherent to the shell surface. Periostracum surface smooth or of closely adjacent, blade-like lamellae that overlay spiral sculpture without giving rise to hair-like projections, or hairy, producing one or several hairs at intersections of lamellae with

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aorta; ct, ctenidium; ddg, duct of the digestive gland; dg, digestive gland; dgL, duct of gland of Leiblein; gL, gland of Leiblein; h, heart; ht, cephalic tentacles; ig, intestinal groove; nep, nephridium; nr, circumoesophageal nerve ring; oe, oesophagus; op, operculum; os, osphradium; ov, ovary; poe, posterior oesophagus; pr, proboscis; prr, proboscis retractors; rhd, proboscis sheath; s, siphon; sd, salivary duct; sg, salivary gland; st, stomach; vL, valve of Leiblein.

Table 8.—*Chlanidota (Pfefferia) chordata* (Strebel, 1908). Measurements of shell characters. Linear measurements in mm ($n = 10$, including holotype).

Character	Mean	σ	Range	Holotype
Shell Length (SL)	27.9	3.5	23.2–34.4	34.7
Body Whorl Length (BWL)	21.9	3.7	16.7–29.7	29.0
Aperture Length (AL)	19.1	2.9	15.3–23.2	21.7
Shell Width (SW)	21.1	3.4	17.2–26.7	23.8
Operculum Length (OL)	12.0	3.3	7.7–16.2	—
BWL/SL	0.79	0.12	0.60–0.89	0.83
AL/SL	0.68	0.05	0.60–0.74	0.62
SW/SL	0.75	0.06	0.68–0.86	0.69
OL/AL	0.61	0.09	0.46–0.73	—
No. spiral cords on:				
Penultimate whorl	5.7	2.4	4–11	5
Body whorl	13	6.3	7–26	12

spiral cords. Operculum large (0.46–0.73 AL), massive, typical of genus.

Ultrastructure.—(Fig. 22C, E) Outermost prismatic layer comprising spiral cords, greatly variable in thickness, ranging from 825 μm in strongly corded specimens (Fig. C) to 58 μm in lightly corded shells (Fig. E). Middle, comarginal layer ranges from 60 to 210 μm , inner, radial layer reaches ≈ 60 μm in thickness.

Anatomy.—Gross anatomy of *C. (P.) chordata* very similar to that of *C. (P.) palliata*. Radular ribbon long (0.66 AL), ≈ 720 μm wide (0.036 AL), triserial (Fig. 22A–B), of ≈ 65 rows of teeth, of which 5 are nascent. Rachidian teeth with deeply arched base, nearly straight lateral sides, 3 large, robust cusps of equal-length. Lateral teeth with 3 cusps, outermost cusp largest, intermediate cusp thinnest and shortest, adjacent to inner cusp. Stomach U-shaped without obvious caecum, too poorly preserved to reveal internal details.

Type locality.—Cumberland Bay, South Georgia, 54°11'S, 36°18'W, in 252–310 m (Sveska Südpolarexp., Sta. 34).

Type material.—Holotype, SMNH 3660

Material examined.—Holotype. R/V *Is-las Orcadas*: South Georgia: Sta. 9, 53°43'30"S, 37°30'06"W, 271–313 m, 12 May 1975, 2 specimens, USNM 901677; Sta. 18, 54°02'30"S, 37°39'36"W, 60–71 m, 15 May 1975, 3 specimens, USNM 901678;

Sta. 19, 54°01'42"S, 37°40'00"W, 46–70 m, 15 May 1975, 3 specimens + 1 shell, USNM 901679; Sta. 20, 54°00'06"S, 37°40'36"W, 68–80 m, 15 May 1975, 4 specimens, USNM 901680; Sta. 22, 54°02'48"S, 37°23'42"W, 66–75 m, 16 May 1975, 3 specimens + 6 shells, USNM 881724; Sta. 25, 53°51'02"S, 36°49'03"W, 199–247 m, 17 May 1975, 1 shell, USNM 901681; Sta. 26, 53°43'06"S, 36°49'18"W, 183–192 m, 17 May 1975, 3 specimens + 3 shells, USNM 881756; Sta. 88, 54°31'45"S, 36°48'42"W, 150–154 m, 7 Jun 1975, 2 specimens + 1 shell, USNM 896287; Sta. 89, 54°44'12"S, 37°11'12"W, 225–265 m, 7 Jun 1975, 6 specimens + 7 shells, USNM 881760; Sta. 90, 54°50'48"S, 37°23'48"W, 223–227 m, 7 Jun 1975, 8 shells, USNM 881762; Sta. 101, 54°14'10"S, 37°54'20"W, 164–183 m, 10 Jun 1975, 1 shell, USNM 901682. R/V *Prof. Siedlecki*: South Georgia: Sta. 20, 53°58'S, 38°42'W, 189–200 m, 2 Dec 1986, 1 shell, USNM 901683; Sta. 37, 54°18'S, 37°54'W, 158–194 m, 5 Dec 1986, 1 shell, USNM 897573; Sta. 83, 54°39'S, 35°49'W, 98–127 m, 11 Dec 1986, 2 specimens + 4 shells, USNM 897534; Sta. 84, 54°28'S, 35°39'W, 231–249 m, 11 Dec 1986, 1 specimen, USNM 897536; Sta. 88, 54°15'S, 35°51'W, 232–254 m, 11 Dec 1986, 2 shells, USNM 897506; Sta. 90, 54°10'S, 35°15'W, 242–262 m, 12 Dec 1986, 1 shell,

USNM 896998; Sta. 91, 54°09'S, 35°55'W, 218–227 m, 12 Dec 1986, 3 specimens, USNM 897450; Sta. 101, 53°47'S, 36°34'W, 263–277 m, 2 shells, USNM 897457; Sta. 105, 53°40'S, 36°48'W, 161–192 m, 14 Dec 1986, 2 specimens + 6 shells, USNM 897515; Sta. 106, 53°44'S, 36°51'W, 178–201 m, 14 Dec 1986, 5 shells, USNM 896985.

Distribution.—Off Southern Georgia (Fig. 22). Living specimens collected at depths from 46 to 313 m.

Remarks.—*Chlanidota* (*Pfefferia*) *chordata* is highly variable in shell morphology, with the extremities of the morphological range appearing very different (compare, e.g., Fig. 21K, J to L, M). Incrementally transitional forms ranging from nearly smooth to highly corded individuals were present in our samples (e.g., Fig. 21M↔L↔F↔A↔D↔H↔J). Specimens from depths (<100 m) (e.g., Fig. 21L, M) tend to have smaller shells with more numerous and more densely spaced spiral cords than specimens from deeper water (>150 m) (e.g., Fig. 21D, H, J). Intermediate specimens between these extremes occur within single dredge hauls at both shallow and deep stations. Specimens with intermediate shell morphology might be confused with *Chlanidota* (*Pfefferia*) *palliat*a (compare Fig. 21F–G with Fig. 17F–G).

Chlanidota (*Pfefferia*) *invenusta*,
new species

Figs. 24–26; Table 9

Chlanidota densesculpta (partim)—Dell, 1990:183, fig. 306.

Description.—Shell (Fig. 23) thick, solid, ovate-rounded. Protoconch, 1½ upper teleoconch whorls eroded. Teleoconch with ≈4 strongly convex whorls. Shoulder rounded. Suture adpressed, deep, wide, nearly channeled. Subsutural rim well pronounced, slightly convex. Spiral sculpture of weak cords (25–40 on body whorl, 5–14 on penultimate whorl) constant in width adapically, of variable width and promi-

nence below shoulder. Axial sculpture limited to fine, often indistinct growth lines. Aperture of moderate height (0.60–0.72 SL), elongate-ovate, deflected from the shell axis by 17–21°. Outer lip thin to thick, evenly rounded, weakly reflected in thick-lipped adults. Outer lip thin and evenly rounded, slightly deflected. Columella short (<½ AL), straight, with strong, long siphonal fold, siphonal region slightly elongated, inflected in some specimens. Callus narrow, thin to thick overlying parietal region, siphonal fasciole, white when thin, greenish-gray at margins when thick. Siphonal notch broad, dorsally recurved, with straight columellar, rounded apertural margins forming borders of fasciole. Apertural margin of siphonal notch gives rise to weak ridge margin. Shell color grayish white. Periostracum (Fig. 24D) light-olive, moderately thick, tightly adherent to shell surface, forming very low, densely spaced lamellae along the growth lines. Operculum (Fig. 23D, H, J, L) large (0.47–0.62 AL), oval, light to dark brown, apical end rounded to weakly tapering, nucleus, terminal, rotated nearly perpendicular to long axis of operculum, posterior edge smooth (Fig. 23d, J), or with weakly (Fig. 23H) to strongly (Fig. 23L) feathered lamellae.

Ultrastructure.—(Fig. 25C) Outer prismatic layer comprises spiral cords, variable in thickness, ranging from ≈80 μm to ≈140 μm, depending on strength of cord. Middle layer comarginal (≈120 μm). Inner layer radial, reaching ≈50 μm in thickness, is the last layer to be deposited, may not be evident in immature specimens (Fig. 25C).

Anatomy.—The gross anatomy of paratype 1 was examined, and found to be similar in all details to that of *C. (P.) palliat*a with the exception that the animal lacked eyes. Radular ribbon (Fig. 24A–B) long, 13.6 mm (0.54 AL), ≈760 μm wide (0.030 AL), triserial, consisting of ≈80 rows, 6 of which are nascent. Rachidian teeth with arched base, straight lateral sides, 3 large, robust cusps, central cusp slightly larger than flanking cusps. Small intermediate ser-

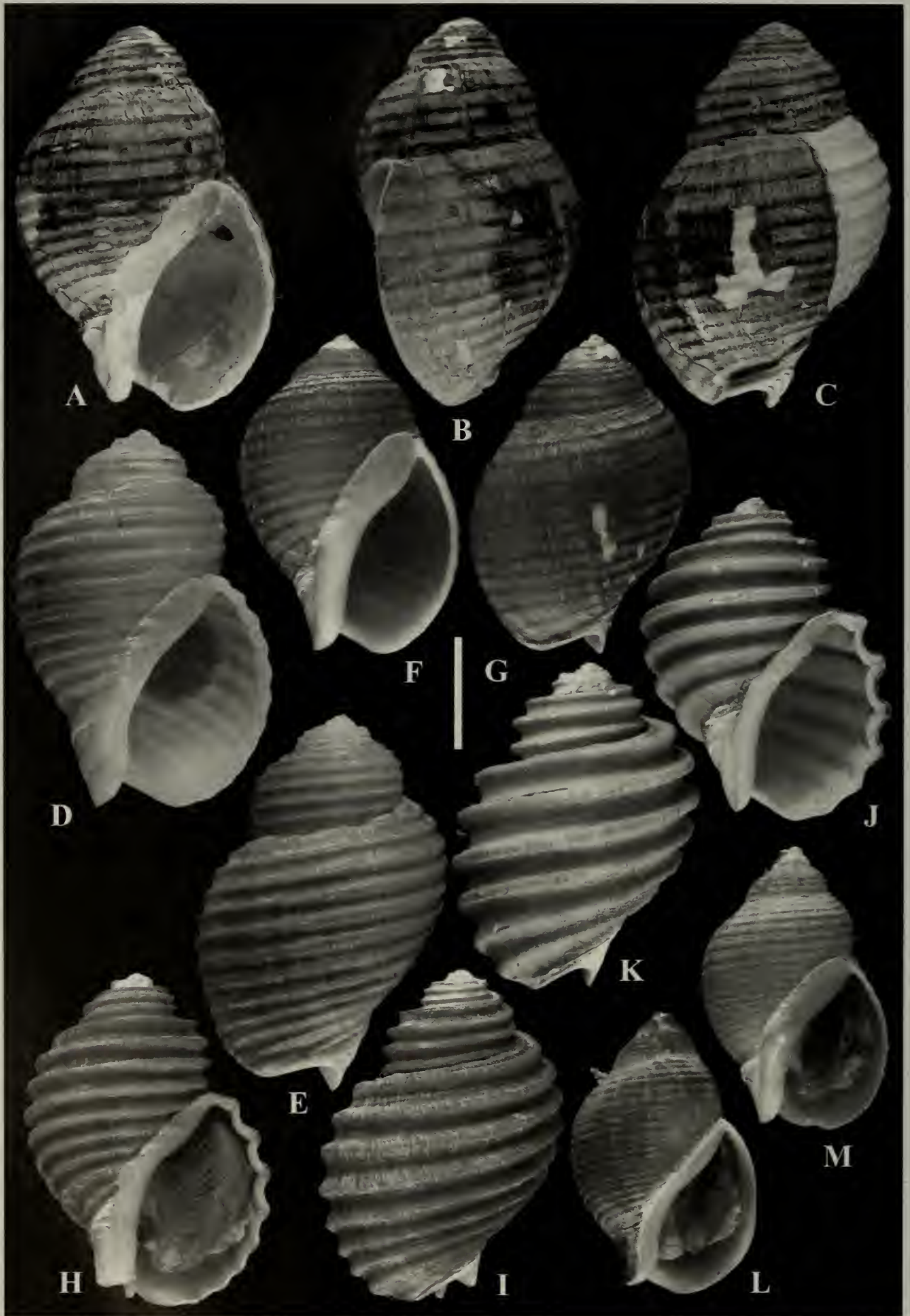


Fig. 21. *Chlanidota (Pfefferia) chordata* (Strebel, 1908). A–C. Holotype, SMNH 3660, Sveska Südpolarexp., Sta. 34, Cumberland Bay, South Georgia, 54°11'S, 36°18'W, in 252–310 m. D, E. R/V *Islas Orcadas*, Sta. 89, South Georgia, 54°44'12"S, 37°11'12"W, in 225–265 m, USNM 881760. F, G. R/V *Islas Orcadas*, Sta. 9, South Georgia, 53°43'30"S, 37°30'06"W, in 271–313 m, USNM 901677. H, I. R/V *Prof. Siedlecki*, Sta. 105, South

ration present between central cusp and right flanking cusp of one specimen. Lateral teeth with 3 cusps, as in genus.

Type locality.—South Georgia Island, 53°31'12"S, 37°50'54"W, in 1267–1599 m (R/V *Islas Orcadas*, Sta. 7).

Type material.—Holotype, USNM 881782, paratypes 1–9, USNM 880280, all from the type locality.

Material examined.—South Georgia: R/V *Islas Orcadas*, Sta. 7, 53°31'12"S, 37°50'54"W, 1267–1599 m, 11 May 1975, Holotype, USNM 881782, paratypes 1–9, USNM 880280, 17 shells, USNM 901684; Sta. 27, 53°34.9'S, 36°47.8'W, 448–872 m, 17 May 1975, 1 specimen, USNM 901685; R/V *Eltanin*: Sta. 731, 53°35'S, 36°28'W, 796–824 m, 11 May 1975, 13 specimens, USNM 896048; Sta. 734, 53°23'S, 37°11'W, 1299–1400 m, 11 May 1975, 4 shells, USNM 870389, 8 specimens, USNM 896049.

Distribution.—Known only from the northwestern coast of South Georgia (Fig. 25). Living material was collected at depths ranging from 448 to 1599 m.

Etymology.—*invenustus* (Lat.)—unattractive.

Remarks.—*Chlanidota* (*Pfefferia*) *invenusta* may be distinguished from the other species in the subgenus *Pfefferia* by its more inflated shell, with a stepped rather than conical spire, more numerous and finer spiral cords, a broader, more rounded aperture, and an operculum in which the feathering along the posterior edge is much narrower to entirely absent. Some specimens superficially resemble *Chlanidota densesculpta*, but may be distinguished on the basis of their larger operculum, thicker shell, more rounded and stepped spires, and proportionally smaller, more rounded, and more deflected apertures.

The nine paratypes collected with the holotype exhibit some variation in shell outline and the number of spiral cords. Smaller specimens tend to have more rounded shells, while the number of spiral cords does not correlate with shell size. Opercula of the smallest specimens are yellow and translucent, and clearly show that the terminal nucleus is coiled, as in *Neobuccinum*.

Species excluded from
Chlanidota sensu lato

Chlanidota smithi Powell, 1958
Fig. 27

Chlanidota smithi Powell, 1958:192, pl. 3, fig. 3; Dell, 1990:177.

Type locality.—Off Enderby Land, 65°50'S, 54°23'E, in 220 m (BANZARE, Sta. 42).

Material examined.—Holotype, SAM D15471 (Fig. 27).

Published records.—BANZARE, Sta. 41, Off Enderby Land, 65°48'S, 53°16'E, 193 m (Powell, 1958:192).

Remarks.—Powell (1958) placed this species in a group with *Chlanidota densesculpta*, *C. vestita*, and *C. pilosa*, but distinguished it from these taxa on the basis of its “disproportionally large,” bulbous protoconch and the almost smooth surface on all whorls. Powell (1958) conjectured that Smith’s (1902) record of *C. vestita* from Cape Adare, 24–26 fm [45–48 m] might represent *C. smithi*. However, Dell (1990: fig. 311) illustrated the Cape Adare specimen and showed it to represent *C. vestita*. Thus, records of *C. smithi* are restricted to Enderby Land. This species differs from typical *Chlanidota* in number of characters, most notably its very large size (SL = 51.5 mm) and very large protoconch. Compari-

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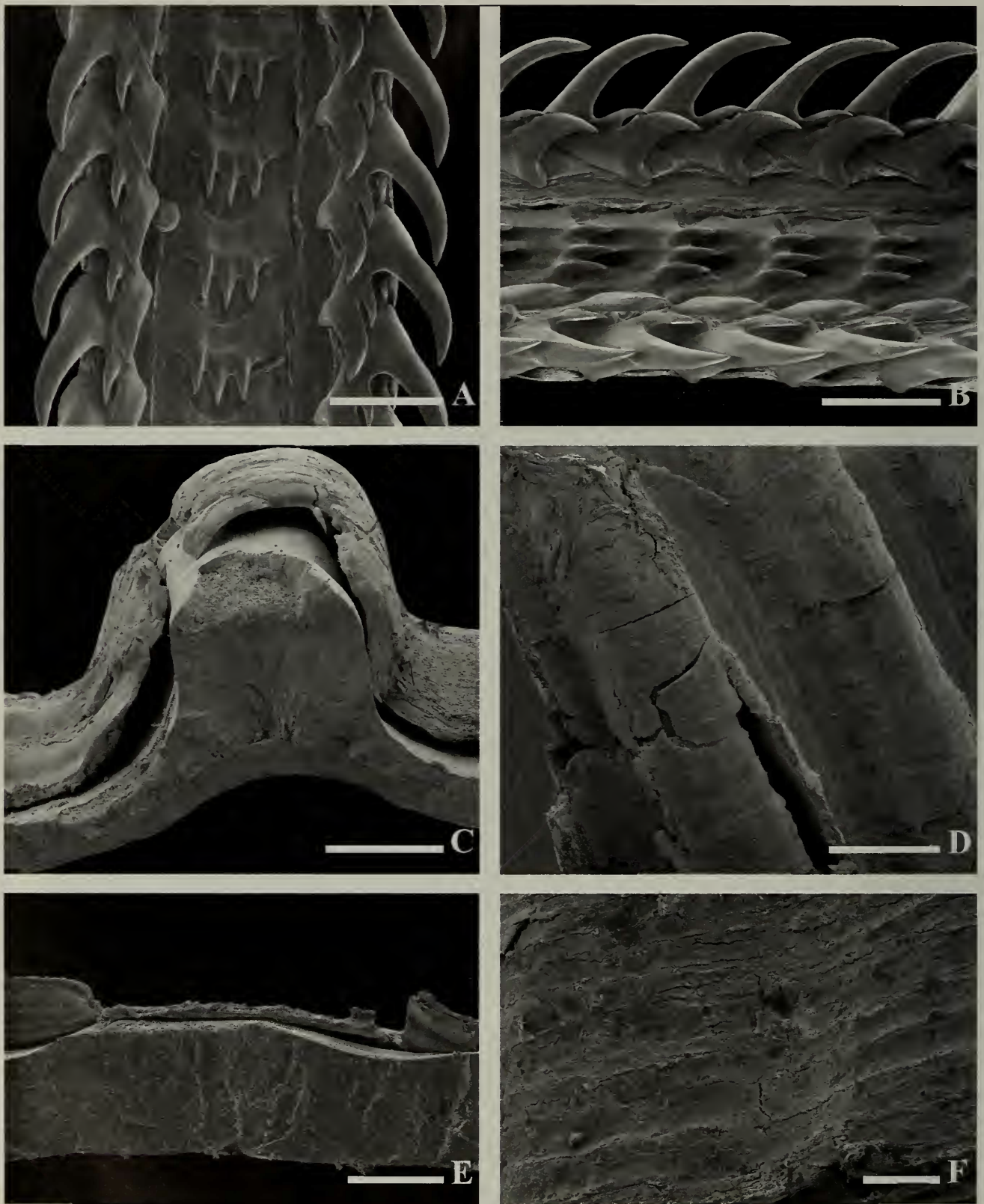


Fig. 22. *Chlanidota (Pfefferia) chordata* (Strebel, 1908). A. Dorsal and B. left lateral (45°) views of the central portion of the radular ribbon taken from specimen in fig. 21F–G. C. Shell ultrastructure and D. periostracum of the strongly corded shell. R/V *Prof. Siedlecki*, Sta. 83, South Georgia, $54^\circ 39'S$, $35^\circ 49'W$, in 98–127 m, USNM 897534. E. Shell ultrastructure and F. periostracum of the weakly corded shell (fig. 20M). Scale bars = $200\ \mu\text{m}$ for A, B, E, F, $500\ \mu\text{m}$ for C, $1000\ \mu\text{m}$ for D.

Table 9.—Measurements of shell characters of the type series of *Chlanidota (Pfefferia) invenusta*, new species.

Character	Holotype	Paratype 1	Paratype 2	Paratype 3	Paratype 4	Paratype 5	Paratype 6	Paratype 7	Paratype 8	Paratype 9	Mean	σ
Shell Length (SL)	38.3	39.6	32.6	38.6	31.8	31.0	36.0	26.5	22.2	19.0	31.6	7.1
Body Whorl Length (BWL)	31.6	31.9	27.3	30.7	25.8	26.3	30.3	22.2	18.7	16.3	26.1	5.5
Shell Width (SW)	26.4	27.2	23.4	25.6	22.9	22.0	25.6	17.4	16.0	14.4	22.1	4.6
Aperture Length (AL)	24.6	25.0	21.9	23.2	19.0	20.1	22.0	18.2	15.6	13.7	20.3	3.7
Operculum Length (OL)	12.4	12.2	10.2	—	11.7	11.7	10.5	8.8	8.0	7.2	10.3	2.0
BWL/SL	0.82	0.81	0.84	0.80	0.81	0.85	0.84	0.84	0.84	0.86	0.83	0.02
AL/SL	0.64	0.63	0.67	0.60	0.60	0.65	0.61	0.69	0.70	0.72	0.64	0.04
SW/SL	0.70	0.69	0.72	0.66	0.72	0.71	0.71	0.67	0.72	0.76	0.70	0.03
OL/AL	0.50	0.49	0.47	—	0.62	0.58	—	0.48	0.51	0.53	0.53	0.06
Number of spiral cords	15	14	16	19	12	11	?	8	8	5	12	4.5
Penultimate whorl	32	26	25	40	24	29	29+	29	38	27	29.9	5.3
Body whorl	3+	3++	3+	3++	3+	3+	3+	2++	2++	2+		
No. whorls												

son of the holotype of *C. smithi* (Fig. 27) with the specimens of *Neobuccinum eatoni* Smith, 1875, clearly reveal a striking conchological similarity between these species. Numanami (1996:146) noted that the majority of specimens of *N. eatoni* taken off Syowa Station (Enderby Land) are obese, with a large, well inflated body whorl. Comparison of Numanami's (1996:fig. 94A, B, D–G) illustrations of *Neobuccinum eatoni* with the holotype of *Chlanidota smithi* leave no doubt that these two taxa are conspecific.

Chlanidota gaini (Lamy, 1910)

Sipho gaini Lamy, 1910:319; Lamy, 1911: 7, pl. 1, figs. 7–8.

Prosipho? gaini Thiele, 1912:262.

?*Chlanidota gaini* Powell, 1951:142.

Chlanidota gaini Carcelles, 1953:191; Dell, 1990:177.

Type locality.—Off King George Island, South Shetlands, in 420 m.

Material examined.—Holotype, NMNH.

Remarks.—"Sipho" *gaini* was provisionally attributed to *Chlanidota* by Powell (1951) and by Carcelles (1953). Dell (1990) considered *Chlanidota gaini* to be a species of uncertain affinity, known only from its holotype.

Examination of the holotype, which had not been illustrated since its description, clearly indicates that this species is referable to the family Conidae (sensu Taylor et al., 1993), and is, in fact, the senior synonym of *Belaturricula antarctica* (Dell, 1990). The composition and relationships of the genus *Belaturricula* are the subject of a separate report (Kantor & Harasewych 1999). Hedley (1916) was the first to surmise the conoidean affinities of *Sipho gaini*, suggesting that it was closely related to *Pontiothauma ergata* Hedley, 1916.

Chlanidota eltanini Dell, 1990

Chlanidota eltanini Dell, 1990:184–5, figs. 290, 292, 297, 314.

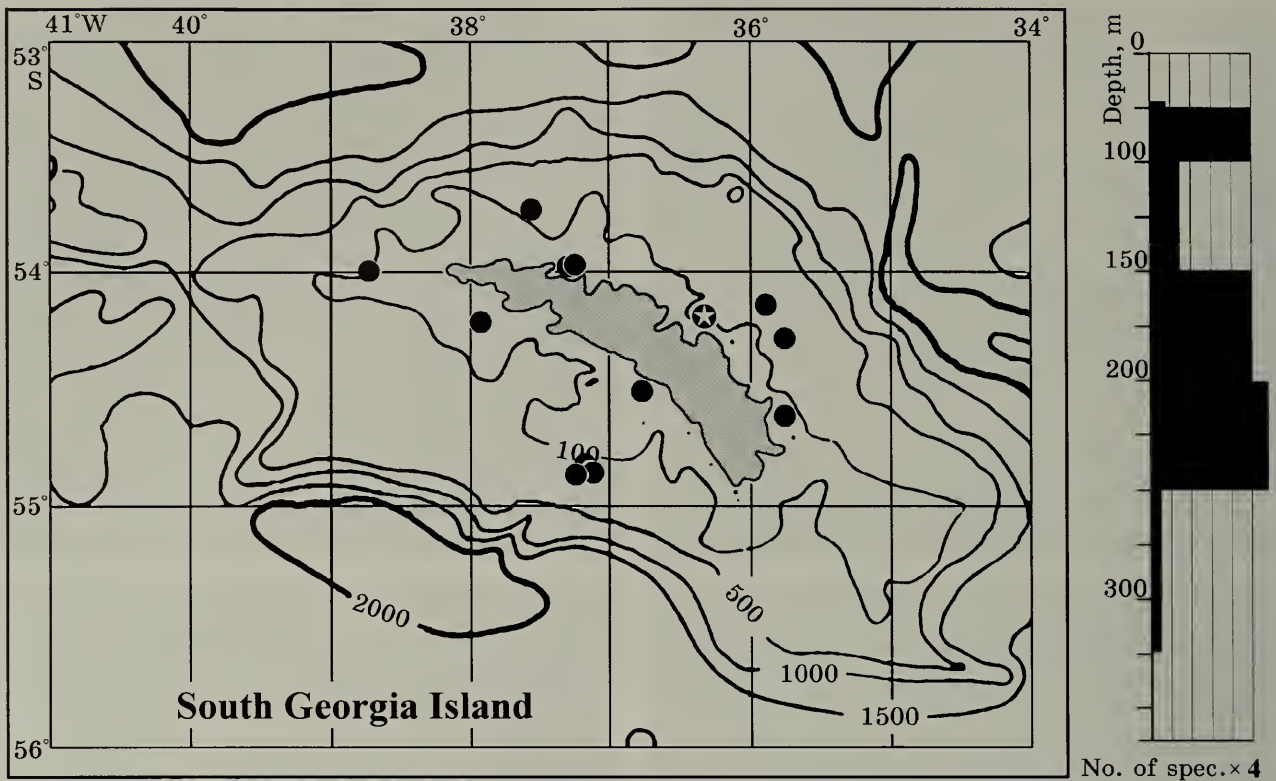


Fig. 23. Geographic distribution and bathymetric range of *Chlanidota* (*Pfefferia*) *chordata* (Strebel, 1908). ☆ = type locality; ● = examined material.

Type locality.—East of Falklands Islands (Islas Malvinas), 51°58'S, 56°38'W, depth 845–646 m (R/V *Eltanin*, Sta. 558).

Type material.—Holotype, USNM 860124, 2 paratypes USNM 860125, 1 paratype NMNZ MF.56613, from the type locality. R/V *Eltanin*: Sta. 557, East of Falkland Islands, 51°56'S, 56°39'W, 855–866 m, 2 paratypes USNM 860126; Sta. 1521, South Atlantic Ocean, 54°09'S, 52°08'W, 419–483 m, 2 paratypes USNM 860127, 1 paratype NMNZ MF.56614.

Remarks.—Dell (1990) described *Chlanidota eltanini*, *C. biscalpta* and *C. polyspeira* from the Magellanic Province. While these three species are likely congeneric, they differ significantly from species assigned to the subgenera *Chlanidota* and *Pfefferia*. Conchologically, these species are readily distinguished by their small (15–16 mm), slender, thick shell, very thin, smooth periostracum, and large (0.6 AL), coiled operculum. We were able to examine the anatomy of *Chlanidota biscalpta*, as well as of a closely related but as yet undescribed species, and found differences in

radular morphology, stomach shape, size of gland of Leiblein, and penis morphology. We provisionally consider these species to be more closely related to *Neobuccinum*, and exclude them from *Chlanidota*.

A revision of this group will be published separately.

Chlanidota biscalpta Dell, 1990

Chlanidota biscalpta Dell, 1990:185, figs. 291, 294, 295, 312.

Type locality.—Burdwood Bank, 53°08'S, 59°23'W, in 578–567 m (R/V *Eltanin*, Sta. 340).

Type material.—Holotype, USNM 860128; R/V *Eltanin*: Sta. 557, East of Falkland Islands (Islas Malvinas), 51°56'S, 56°39'W, 855–866 m, 6 paratypes USNM 860129, 1 paratype NMNZ MF.56615; Sta. 740, off Cape Horn, 56°06'S, 66°19'W, 384–494 m, 2 paratypes USNM 860130, 1 paratype NMNZ MF.56616.

Remarks.—See remarks under *Chlanidota eltanini* Dell, 1990.

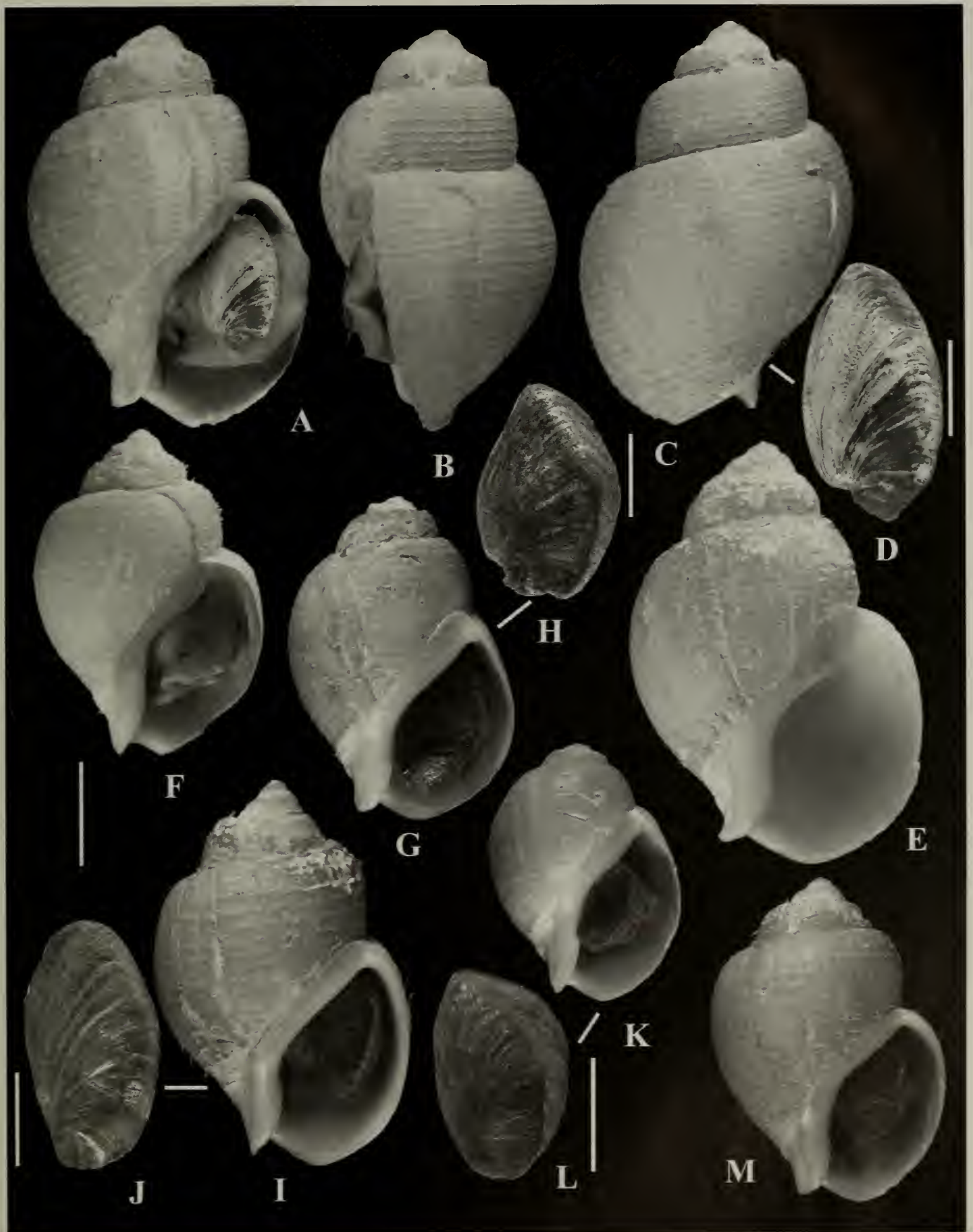


Fig. 24. *Chlanidota* (*Pfefferia*) *invenusta* new species. A–C. holotype, USNM 881782, R/V *Islas Orcadas*, Sta. 7, South Georgia, 53°31'12"S, 37°50'54"W, in 1267–1599 m. D. Operculum of holotype, enlarged. E. Paratype 1, (anatomy studied), and F. paratype 5, USNM 880280, both from type locality. G. H. Specimen with narrowly rimmed operculum. I, J, M. Specimens with smooth operculum. K, L. Specimen with broadly rimmed operculum, all from R/V *Eltanin*, Sta. 734, South Georgia, 53°23'S, 37°11'W, in 1299–1400 m, USNM 896049. Scale bar = 1 cm for shells, 5 mm for opercula.

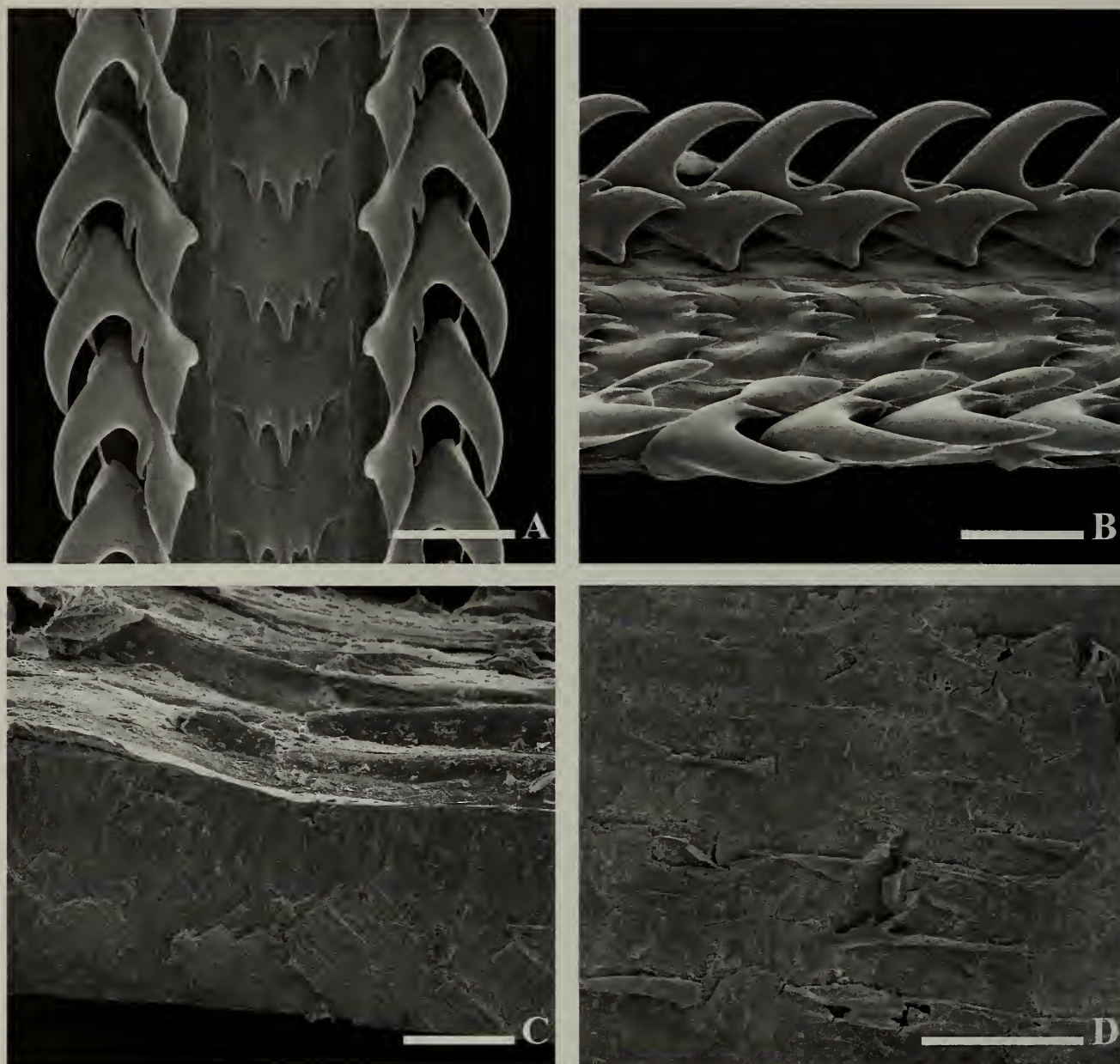


Fig. 25. *Chlanidota (Pfefferia) invenusta*, new species. A. Dorsal and B. left lateral (45°) views of the central portion of the radular ribbon of paratype 1 (Fig. 24E). C. Shell ultrastructure, and D. periostracum of the paratype 5 (Fig. 24F). Scale bar = 200 μm for A, B, 100 μm for C, 500 μm for D.

Chlanidota polyspeira Dell, 1990

Chlanidota polyspeira Dell, 1990:186, figs. 292, 293, 313.

Type locality.—Patagonian Shelf, 54°04'S, 63°35'W, depth 247–293 m (R/V *Eltanin* Sta. 369).

Type material.—Holotype, USNM 860131, 3 paratypes, USNM 860132, 1 paratype NMNZ MF.56617, all from the type locality.

Remarks.—See remarks to *Chlanidota eltanini* Dell, 1990.

Discussion

Buccinoidean classification has traditionally been based on a combination of shell, opercular, and radular characters, and these structures are well documented for the majority of Antarctic genera (e.g., Thiele 1904, Powell 1951, Hain 1989, Dell 1990, Numanami 1996). Ponder (1974) reported that most organ systems were weakly differentiated among buccinoidean higher taxa, and that it was difficult to identify anatomical features that could be used to seg-

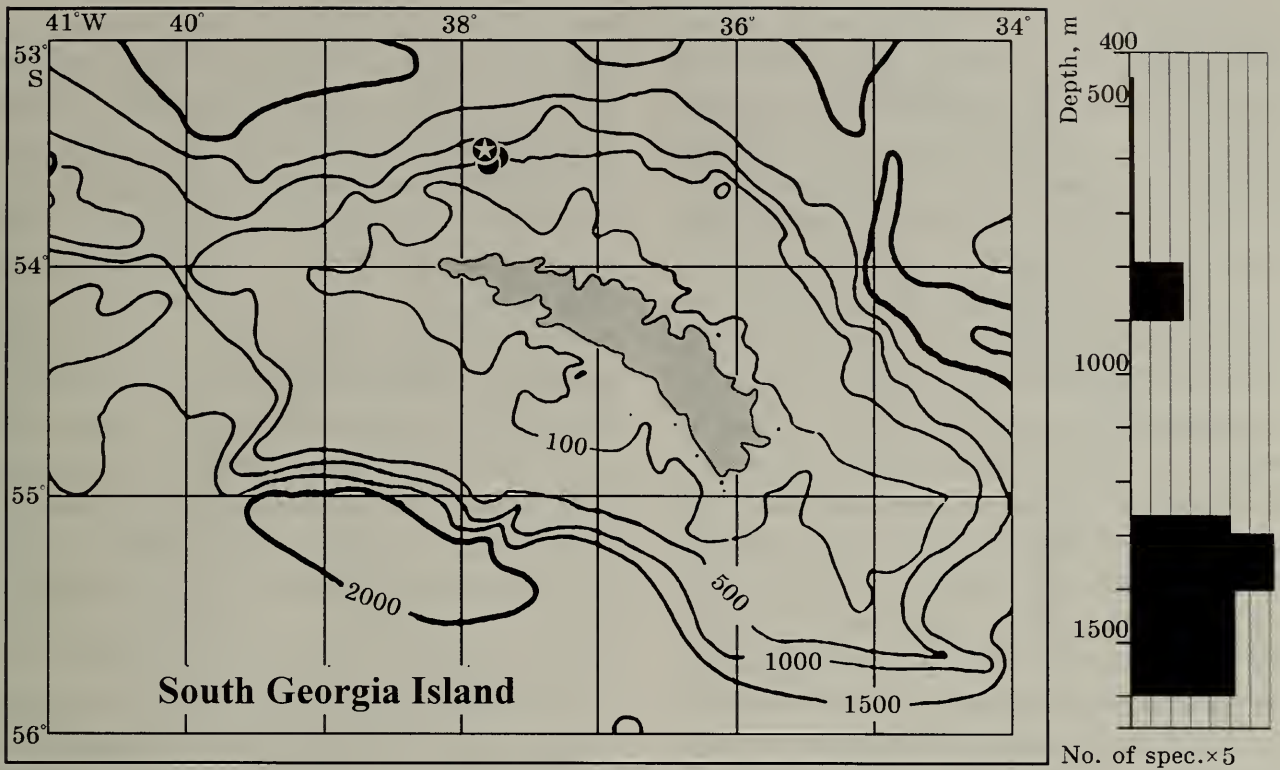


Fig. 26. Geographic distribution and bathymetric range of *Chlanidota (Pfefferia) invenusta*, new species. ★ = type locality, ● = examined material.

regate them reliably. More recently, Hara-sewych (1990) identified several characters, including the morphology of the gland of Leiblein and the presence of an ingesting

gland, that vary among buccinoideans and may be phylogenetically informative. While there have been a substantial number of anatomical investigations of boreal (e.g., Da-



Fig. 27. *Chlanidota smithi* Powell, 1958. Holotype, SAM D15471, BANZARE Sta. 42, Off Enderby Land, 65°50'S, 54°23'E, in 220 m. Scale bar = 1 cm.

kin 1912; Lus 1978, 1981, 1989; Kantor 1988, 1990), tropical (e.g., Marcus & Marcus 1962, 1964) and deep-sea (e.g., Ponder 1968, Harasewych 1990) buccinoidean taxa, the anatomy of Antarctic representatives has not previously been studied in any detail.

It is not surprising that *Chlanidota* shares many anatomical features with the boreal family Buccinidae, among them similar arrangements of the mantle cavity organs, reproductive system, and many characters of the digestive system. Characters such as a long, thick proboscis and fused salivary glands occur in *Chlanidota* as well as in the buccinid taxa *Habevolutopsius* (Kantor 1990) and Ancistrolepidinae (Kantor 1988). The stomach of *Chlanidota*, however, differs from that of most Buccinidae in being broadly U-shaped and in lacking a caecum. The caecum, or posterior mixing area, is usually well developed in boreal Buccinidae, and is sometimes very large (e.g., in *Volutopsius*, subfamily Volutopsiinae), making the stomach appear sac-like. The stomach of Southern Hemisphere taxa, such as *Penion adustus* (Philippi, 1845) (Ponder 1973) and *Ratifusus mestayerae* (Iredale 1915) (Ponder 1968), which had been assigned to Buccinulidae by Powell (1961), also lack a caecum.

The northern Atlantic buccinid *Colus gracilis* (da Costa 1778) is unusual in lacking a gastric caecum (Smith 1967). However, its stomach differs from the stomach of *Chlanidota* in having a cuticularized shield and a distinct sphincter between the oesophagus and stomach. The stomach epithelium of *Colus gracilis* is glandular and darker than the esophageal epithelium, while in *Chlanidota* the epithelial lining of the esophagus is dark and that of the stomach is lighter.

Unlike all other *Chlanidota* and *Pfefferia*, the stomach of *Chlanidota* (*Chlanidota*) *paucispiralis* has a small enlargement (Fig. 14, pm) corresponding in position to the caecum of *Neptunea* (Smith 1967), *Buccinum* (Medinskaya 1993) and other boreal

buccinids. It is still not clear, whether the presence of a gastric caecum is an advanced or plesiomorphic character, as the structure occurs in many neogastropod families (e.g., Buccinidae, Volutomitridae, Muricidae, Mitridae) but is absent in others (e.g., Columbellidae, Volutidae, Cancellariidae and all Conoidea).

The posterior oesophagus of *Chlanidota* is greatly enlarged, thick-walled, and lined with tall epithelial folds (e.g. Fig. 5H), which are darker than the rest of esophageal epithelium. The transition between the posterior oesophagus and the stomach is clearly evident on dissection, as it is marked by a color change of the epithelium near the posterior duct of the digestive gland.

The morphology of the radula and major organ systems is remarkably invariant in all of the species of *Chlanidota* and *Pfefferia* that we examined. The only exceptions were the presence of a small caecum in *C. (C.) paucispiralis* and of separate rather than fused salivary glands in *C. (C.) signeyana*. Preliminary dissections of other Antarctic buccinulids generally regarded as being closely related to *Chlanidota* (e.g., *Neobuccinum eatoni*, "*Chlanidota*" *bisculpta*, see above) revealed significant differences in their alimentary and male reproductive systems, providing support for reducing *Pfefferia* to a subgenus of *Chlanidota*.

The morphology of the operculum of *Chlanidota* (*Pfefferia*) is both striking and unique within Neogastropoda. The mechanism by which the characteristic "feathered" margin is formed along the posterior edge of the operculum is readily inferred. Newly secreted layers of conchiolin are broader adapically than abapically, and are attached to the posterior edge of the operculum only along their proximal margins. While operculum morphology is constant in *C. (P.) palliata* and *C. (P.) chordata*, it varies considerably in the newly described *C. (P.) invenusta*. Juveniles of *C. (P.) invenusta* have an operculum with a "feathered" margin. The width of this margin de-

creases with increasing shell size, the margin disappearing entirely in large specimens (see Fig. 24L→H→J→D). The size of the operculum of *C. (P.) invenusta* (0.47–0.62 AL) is larger than in any species of *Chlanidota* (*Chlanidota*) (0.18–0.37 AL), comparable to that of *C. (P.) chordata* (0.46–0.73 AL), but smaller than that of *C. (P.) elata* (0.68–0.78 AL). The large operculum of *Chlanidota (Pfefferia)* allows it to seal the aperture tightly when the animal withdraws into its shell (e.g., Figs. 17F, 21H), while its “feathered” posterior margin provides a flexible, tight seal against the outer lip. In contrast, the small size of the operculum in *Chlanidota* s.s. precludes its utility for sealing the aperture. The decrease in relative size and “degree of feathering” of the operculum in *C. (P.) invenusta* with increasing shell size, suggests that the ability to seal the aperture tightly diminishes in importance as the animal grows.

While the anatomy and radular morphology are largely invariant in *Chlanidota* and *Pfefferia*, shell shape and the strength and number of spiral cords and threads vary considerably. The limited number of specimens available to previous workers has, in a few instances, led to the description of species based on differences that now appear to fall within a broad continuum of morphological variability revealed by larger sample sizes spanning wider geographical areas.

As restricted in this paper, the genus *Chlanidota* is confined to the Antarctic region, with only the type species ranging slightly beyond the Antarctic Convergence. The present revision reduces the number of recognized species within *Chlanidota*. Nevertheless, it remains the second most diverse buccinoidean genus (following *Prosipho*) in Antarctic waters.

Of the eight recognized species in the genus *Chlanidota*, only *C. (C.) signeyana* has a broad circum-Antarctic distribution (although records from the poorly sampled Ross Quadrant are lacking). Except for a single record of *C. (C.) vestita* from Cape

Adare, all remaining species of *Chlanidota* are restricted to subAntarctic islands, with two species of *Chlanidota* sensu stricto, and all three species of *Pfefferia* endemic to South Georgia. Of the species inhabiting subAntarctic islands, most are sublittoral, and only *Chlanidota (Pfefferia) invenusta* is restricted to bathyal depths. In contrast, the circum-Antarctic *C. signeyana* has a broad bathymetric range (30–1116 m).

The protoconchs of all specimens of *Chlanidota* were severely eroded, hampering inference of developmental mode. However, most polar species, including buccinoideans, develop directly without a pelagic larval stage (Thorson 1946). Thus, it seems likely that the island populations of *Chlanidota* are vicariant isolates from a more broadly ranging species.

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